Cache Protection and Decision Making in the Cape Ground Squirrel (*Xerus inauris*)

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Summary

Caching food provides a variety of benefits to an individual, such as the build up of reserves for periods when resources are depleted or to gain a disproportionate amount of an ephemeral resource. One of the risks to adopting this strategy is the potential for theft from food stores, by both conspecifics and/or other species. To reduce this theft, some species have evolved a range of cache protection mechanisms, such as placing food out of site of competitors. In this thesis, I examined various cache protection and decision-making processes exhibited by the Cape ground squirrel (*Xerus inauris*), a social rodent. Due to the sociality of this species, and therefore, the potential for high rates of cache loss, I predicted they would use a diverse range of behaviours to increase the survivability of stored food.

I first described the natural caching behaviours of the Cape ground squirrel in their natural habitat. This species increased caching frequency just after the heaviest periods of rainfall, indicating that this behaviour might be controlled by the availability of food. They cache around a central burrow system, which classifies their cache type as "scatter hoarding". In the second study, I investigated the effect of group size on caching and recovery behaviours. Group size in these ground squirrels showed daily fluctuations, and an increased number of individuals in a group had a negative impact on food cache survival. In response to fluctuations in group size, individuals did not change the spatial arrangement of caches, but I argued that this arrangement was a by-product of optimal cache placement and not a method to protect caches. With increased social competition, the ground squirrels seemed to maximise payoffs from food by consuming rather than caching items. The third study, focused on determining whether the cachers were sensitive to the attentive state of nearby conspecifics. Conspecifics were often observed competing with cachers immediately after a cache was deposited, and therefore ensuring audience members are inattentive to the cache event would decrease the chance a cache was stolen. There was a strong preference for individuals to cache when audience members were inattentive to the cache event. In addition, higher ranked individuals showed less sensitivity to these audience effects, possibly due to their ability to defend food items from conspecifics. In the fourth study I presented individuals with a choice between two food items of differing value: one item that was always artificially removed when cached and the other item that was not removed when cached. Although the two items only varied with respects to the payoff in caching, individuals reduced the amount of the removed items they both consumed or cached during the choice presentations. This avoidance to choose the removed food occurred over time, indicating that individuals were using information about the item's payoff during cache recovery and this then impacted on successive decisions. Due to the lack of obvious landmarks at the study site, in the last experiment, I predicted that individuals might use positional cues from the sun as a reference point when caching and recovering food items. When caching food, individuals moved at consistent offset angles from the sun, moving in straight lines from the provisioning point to the cache point. When recovering food, individuals displayed some flexibility in the use of solar cues, which allowed them to retrieve food more efficiently. Food was retrieved sooner if there were a higher number of individuals present in the group.

Overall, this thesis highlights the variety of decision-making processes individuals must undertake when caching food to ensure maximum profitability. I answered a number of questions on when animals cache, the decisions about what to cache and where to place caches. As this species is social, this decision-making is highly influenced by group members. This thesis provides much needed knowledge on the cache protection strategies used by mammals, where the majority of work has been conducted on birds. Research such as this will hopefully encourage other studies on mammals to determine how social living can lead to the evolution of counterstrategies to protect food stores.

Zusammenfassung

Das Verstecken von Futter bietet einige Vorteile, wie das Anlegen von Vorräten um Zeiten der Dürre zu überbrücken, oder das Speichern von überproportionalen Mengen von saisonal vorkommenden Ressourcen. Ein Risiko dieser Strategie ist die Möglichkeit das Artgenossen oder Tiere anderer Arten die angelegten Vorräte stehlen. Um das Risiko des Diebstahls zu verringern, haben verschiedene Arten Schutzmechanismen evolviert, wie zum Beispiel das Plazieren des Futters außerhalb der Sichtweite von Konkurrenten. In meiner Doktorarbeit habe ich unterschiedliche Arten der Vorratssicherung sowie unterschiedliche Entscheidungsprozesse eines sozialen Nagetieres, dem Kap-Borstenhörnchen (*Xerus inauris*), untersucht. Da diese Art in sozialen Gruppen lebt, und damit wahrscheinlich eine hohe Verlustrate angelegter Vorräte besteht, erwartete ich, dass Kap-Borstenhörnchen verschiedene Verhaltensweisen nutzen um die Beständigkeit ihrer Vorräte zu erhöhen.

Zuerst beschreibe ich die natürlichen Verhalten der Kap-Borsteenhörnchen bei der Anlage von Vorräten in ihrem natürlichen Lebensarum. Diese Art erhöhte die Rate des Versteckens von Vorräten nach Zeiten mit starkem Regen, was andeutet, dass dieses Verhalten von dem Vorhandensein des Futters abhängig ist. Diese verteilt Art verteilt die unterschiedlichen Verstecke um eine zentrale Wohnhöhle, weshalb ihre Art der Vorratsanlage als „scatter-hoarding“ bezeichnet werden kann. Im zweiten Kapitel habe ich untersucht, wie die Größe der sozialen Gruppe das Anlegen und Wiederfinden von Vorräten beeinflusst. Die Gruppengröße verändert sich über den Tag hinweg und eine grössere Anzahl an Tieren in der Gruppe hatte einen negativen Einfluss auf die Wahrscheinlichkeit einen angelegten Vorrat wiederzufinden. Kap-Borstenhörnchen reagierten auf Änderungen der Gruppengröße nicht mit einer Änderung der räumlichen Anordnung ihrer Verstecke. Deshalb argumentiere ich, dass die Anordnung der Verstecke ein Nebenprodukt der optimalen Plazierung ist und nicht als Methode dient um die Verstecke zu schützen. Bei einer erhöhten Konkurrenz durch Artgenossen ist eine Möglichkeit der Gewinnmaximierung das Futter zu verzehren anstatt es zu verstecken, eine Strategie die bei Kap-Borstenhörnchen beobachtet wurde. Im dritten Kapitel untersuche ich, ob Tiere die gerade einen Vorrat anlegen die Aufmerksamkeit räumlicher naher Artgenossen wahrnehmen. Artgenossen wurden häufig dabei beobachtet, wie sie direkt nachdem ein Tier Futter versteckt hatte mit diesem um das Versteck kämpften. Dementsprechend würde sich die Wahrscheinlichkeit verstecktes Futter zu verlieren verringern, wenn versteckende Tiere sicher stellten, dass mögliche Zuschauer gerade unaufmerksam sind. Kap-Borstenhörnchen zeigten eine starke Präferenz dafür Futter genau dann zu verstecken, wenn mögliche Zuschauer unaufmerksam waren. Außerdem konnte ich zeigen, dass höherrangige Tiere weniger empfindlich auf mögliche Zuschauer reagierten, möglicherweise da sie die Fähigkeit besitzen Futter vor Artgenossen zu verteidigen. Im vierten Kapitel habe ich Tiere vor die Wahl zwischen zwei unterschiedlichen Futtertypen gestellt, wobei die Futterstücke eines Typs immer künstlich entfernt wurde, nachdem es versteckt worden war und das andere nicht. Obwohl sich die zwei Futtertypen nur hinsichtlich ihres Gewinns beim Verstecken unterschieden, verzehrten und versteckten die Individuen die Futterstücke vom Typen welches nach dem Verstecken entfernt wurde, deutlich weniger. Diese Vermeidung des wieder entfernten Futtertypen geschah erst nach einer Weile, was darauf hindeutet, dass die Individuen die Information über den Gewinn dieses Futterstückes beim Leeren des Versteckes abschätzen und für zukünftige Entscheidungen nutzen. Im letzten Kapitel testete ich ob Kap-Borstenhörnchen die Sonne als Referenzpunkt nutzen wenn sie Futter verstecken oder es wiederfinden, da auf dem Gelände andere offensichtliche Orientierungspunkte fehlen. Beim Verstecken von Futter bewegten sich die Tiere immer mit einem konstant verschobenen Winkel zur Sonne, und bewegten sich dabei gleichzeitig auf geraden Linien zwischen der Futterquelle und dem Ort des Verstecks. Beim Wiederfinden des Futters zeigten die Tiere Flexibilität bei der Nutzung der Sonne als Orientierungshilfe und entfernten Futter schneller wenn mehr Tiere in der Gruppe anwesend waren.

Insgesamt zeigt diese Doktorarbeit die Vielfältigkeit der Entscheidungen welche Tiere treffen müssen wenn sie Vorräte anlegen, um den Gewinn zu maximieren. Ich habe verschiedene Fragen beantwortet, wie zum Beispiel wann die Tiere Futter verstecken, über die Entscheidungen was sie verstecken und wo sie ihre Verstecke plazieren. Da dies eine sehr gesellige Art ist, sind diese Entscheidungen stark von den Artgenossen in der Gruppe abhängig. Die meiste Forschung über Strategien zum Schutz von angelegten Vorräten wurde bisher an Vögeln gemacht, daher liefert diese Arbeit dringend benötigtes Wissen über diese Strategien bei Säugetieren. Forschung wie diese ermutigt hoffentlich andere Studien an Säugetieren um herauszufinden, wie das Leben in sozialen Gruppen zur Evolution von Strategien zum Schutz von Vorräten führen kann.

General introduction

1. General introduction

Food caching, also known as hoarding or storing, occurs when animals delay consumption of a food item and conceal it, recovering at a later time (Vander Wall 1990). Many animal species cache food for a variety of different reasons (Vander Wall 1990) including storing food for when natural stocks are reduced (Pravosudov & Grubb 1997) and protecting food resources from competitors (Balme et al. 2007). Cached food items can often be buried at a higher rate than they can be consumed (Clarkson et al. 1986; Jacobs 1992) and this allows individuals to acquire a greater proportion of a resource than a non-storer (Dally et al. 2006). If caching is abundantly evident within a species then we can assume that there is an adaptive function, where recovery of caches, analogous to energy return is higher than cache loss (Andersson & Krebs 1978, Stapanian & Smith 1978, Vander Wall 2003).

$$p > \frac{C}{G} + p_r m. \qquad (1)$$

Andersson & Krebs (1978) constructed a simplistic model (*1*) to test under what circumstances caching can become an evolutionary stable strategy (ESS). The model states that the probability of recovering a cache (p_r) needs to be greater than the fitness gained through eating (C) divided by the cost of hoarding that item (G) plus the loss factor times the number of items not hoarded (m). Moremo et al. (1981), argued that p is a dyadic factor; the probability that the food remains available until needed and that the cachers find the food. The model (*1*) describes under what conditions caching can become an ESS in solitary species. For social species, Andersson & Krebs (1978) adjusted the model to include aspects such as number of caches, and pilferers and the number of individuals within a social group. This idea suggests that cachers can manipulate p in two ways through cache recovery (reviewed in Vander Wall 1990) and cache protection (reviewed in Dally et al. 2006) behaviours. However, even where high cache loss occurs, individuals can still benefit from caching, where theft from other competitors stores is high ("reciprocal pilferage" hypothesis, Vander Wall 2003). As cache loss to conspecifics may be higher in social living than more solitary living species (Vander Wall 2003), selection pressures may have caused individuals to engage in behaviours to overcome and/or reduce this loss. This can be seen through the evolution of various cache protection strategies (reviewed in Dally et al. 2004) such as caching items out of site of conspecifics (Bugnyar & Kotrschal 2002) at several locations throughout a home range (Daly et al. 1992), re-cached out of site of competitors (Emery et al. 2004) and making false caches to potentially “deceive” competitors (Steele et al. 2008). Some of these cache protection strategies have been argued to be under cognitive control, for example food-caching corvids have

been suggested to show behaviours such as future planning, which were previously thought to be solely confined to humans (Grodzinski & Clayton 2010).

More often than not, food resources are ephemeral and therefore any hesitation to utilise them may result in reduced benefits. Caching of these food items will result in a build up of such resources, which can be eaten over a short period (reviewed in Dally et al. 2006) or provide reserves over a longer time period (Balda & Bateman 1971). However, here a paradox exists, as if an animal caches all of the resource in areas where conspecifics are present, high cache loss is likely to occur (Vander Wall 2003). Aside from employing various counteracting protection strategies, cachers have been shown to utilise a variety of responses in relation to potential pilfers, even demonstrating behaviour such as audience member discrimination (Leaver et al. 2007; Pravosudov 2008). Mountain chickadees (*Poecile gambeli*) for example, make caching decisions based on the identity of the audience member present. They often cache directly in front of perceived non-pilfering heterospecifics and employ more protection mechanisms when potential pilferers are present (Pravosudov 2008). Items may also be directly eaten when an audience member poses a threat in terms of them pilfering the item (Carrascal & Moreno 1993; Dally et al. 2006). These flexible decision-making behaviours therefore allow individuals to maximise energy gains from the resource, either through consumption or storage.

Even where animals employ cache protection strategies, there is still a risk of items being removed by pilferers when they are randomly foraging through a space (Stone & Baker 1989). However, through repeated learning from caching over time, animals can gather information on what behaviours reduce cache theft under certain social settings (Stone & Baker 1989). Additionally, animals may also learn what food items provide the best returns when cached (Clayton et al. 2005; de Kort et al. 2007), whether the item is removed by competitors (de Kort et al. 2007) or merely degrades over time (Clayton et al. 2005; de Kort et al. 2007). The processes involved in sequestering this information are complex, as animals must acquire an understanding of under what circumstances caches are lost and then alter their behaviour accordingly (Clayton et al. 2005). This has led some authors to suggest these behaviours may be controlled by complex cognitive processing, such as 'episodic-like' memory (Grodzinski & Clayton 2010) and exclusion performance (Schloegl et al. 2009) for example. However, because the single theft of a food item may not predict future outcomes of caching that item, it may pay for individuals to still cache under those conditions and only show a response where there is successive theft. This may therefore suggest these behaviours are

not under cognitive control, but rather as a by product associative learning mechanisms if the costs of caching an item are learnt overtime (Shettleworth 1999).

When individuals engage in cache protection strategies, they must balance the benefits these bring to secure a food resource with their ability to recover such a resource. Animals may therefore benefit from placing items in locations that allow for easy re-orientation, using cues in their environment integrated with their spatial memory (Sherry & Duff 1996). As we find caching species in varied habitats, the cues animals may use to orientate to and from cache sites could range from utilising nearby landmarks (Sherry & Duff 1996), distal landmarks (Brodbeck 1994) and even celestial cues such as the sun (Wiltschko & Balda 1989; Wiltschko et al. 1999). The type of cues animals may use is highly dependent on the environment and what information animals can encode and use (Freas et al. 2012). To reduce spatial orientation errors, animals have been known to amalgamate information from a number of different cues to increase accuracy, which is known as the "multiple bearings hypothesis" (Kamil & Cheng 2001; Gould et al. 2010) . In addition to this, a number of animals have been shown to have flexible cue use, switching between cues in a hierarchical manner, where information from the primary cue is corrupted or lost (Waisman & Jacobs 2008) .

Specific research on related taxa

In their review on cache protection strategies, Dally et al. (2006) emphasize the need for studies on mammals due to an evident bias towards research on corvids and other bird taxa. A number of mammalian studies have shown that individuals show flexibility in their caching decisions and how this is affected by the presence or behaviour of competitors, both con- and hetero-specific (Jenkins et al. 1995; Preston & Jacobs 2005; Wang et al. 2011; Luo et al. 2014 for example). However, the examples mentioned focus on species with a mainly solitary lifestyle, whereas there is a need for studies examining these behaviours in more social species. In solitary species with overlapping ranges such as the grey squirrel (*Sciurus carolinensis*), protection methods such as being sensitive to audience effects (Leaver et al. 2007) and false caching (Steele et al. 2008) have been described. Where social living species have been examined, a number of studies have shown that caches are usually made communally in a central store which all group members have access to, as the benefits of this socially mediated storing behaviour may outweigh the costs of selfish caching (Wolff & Lidicker 1981; Zhong et al. 2007). One key area that needs addressing is how social rodent species that do not store communally, protect their caches from conspecific group members. Whilst there is a paucity of studies on decision making with regards to cache protection in rodents, cache patterns and recovery behaviours have

received a great deal of attention (Vander Wall 1990; Gould et al. 2010). With caching patterns, studies have examined decisions about where to locate caches to maximise benefits (Stapanian & Smith 1978), what to cache (Cheng et al. 2005) and when (Vander Wall 1990) for example. Studies on cache recovery in rodents have mainly focused on the orientation behaviour, identifying the cues rodents use when placing and removing cached food (Waisman & Jacobs 2008; Bruck & Mateo 2010).

2. Study species

Cape ground squirrels are medium sized rodents that weigh between 500-700g at maturity that inhabit arid areas of Southern Africa (Figure 1). They are highly social, although not cooperative in nature, and can live in groups of up to 19 individuals (Waterman 1995). These groups typically consist of 1-3 reproductively active adult females and 9 subadults of either sex (Hillegass et al. 2008). Males disperse at around 16 months,

Figure 1: A mature adult male Cape ground squirrel.

but may delay this, staying within their natal group and being reproductively active within this group until they are 1-2 years of age. Groups of males may form coalitions with a large territory size often encompassing a number of mixed groups as described above. These males prospect around this range but normally sleep independently of the mixed groups. At the study site of this project, ground squirrels form mixed groups where both adult males and females interact and sleep in the same burrow system (JS personal observation). Within these groups, there are stable intersexual dominance hierarchies that are not linear in form but are structured (unpublished data). At maturity, ground squirrels show sexual dimorphism, with males typically

being larger in size than females (1.08:1.0, Waterman 1996). Sexing individuals is easy due to the large testis size in males, indicating that they are under intense sexual selection (Waterman 1995).

3. Study site

This study was undertaken at the Kuruman River Reserve in South Africa (26°858' S, 21°490' E), the site of the Kalahari Meerkat Project. The reserve is located in the green Kalahari (Figure 2), a semi-arid region of sand dunes and flat terraces, with sparse vegetation (Clutton-Brock et al. 2001).

Figure 2: The location of the study site within South Africa. The enlarged section shows an example of the habitat found on the reserve.

4. Aims of the study

The highly social nature of the ground squirrels makes studies on caching behaviour particularly appealing as there may be strong selection for individuals to engage in behaviours to reduce cache theft, not occurring in less social species. Furthermore, as this species lives in an arid environment, competition for resources may

be more elevated than in habitats where resources are saturated. The use of such a species will further our understanding of the dynamics of caching and decision making in a social species, where previous research has mainly examined these aspects in various bird species (Dally et al. 2006).

5. Thesis outline

The main objective of my thesis was to examine decision-making within the context of cache protection in a social animal. A combination of observational studies and experiments were undertaken to test these objectives in the field. As no existing studies on Cape ground squirrel caching behaviour have been undertaken, in **chapter 1**, I aimed to describe this behaviour in terms of its temporal/spatial occurrence and what might affect the decision to cache. A number of studies have highlighted that there are both temporal (Roubik 1982) and spatial variations (White & Geluso 2012) in caching behaviour within a species. The motivation to cache has been shown to be affected by a number of factors, such as for periods when natural stocks are low (Vander Wall 1990) or protecting stores from competitors (Balme et al. 2007). In the Kalahari, resources are often spatially distributed and ephemeral, as bonanza resources such as seeds masts are quickly utilised by a range of species. As the Kalahari shows strong seasonality and sporadic rainfall, I predicted that individuals would cache more in the winter months when food stocks are reduced. Furthermore, I expected that caching would only occur when individuals had already consumed large amount of resources, using caching to secure further food during this period of satiation.

Caching in the presence of conspecifics is hazardous due to the risk of a food item being stolen (Stone & Baker 1989). The effect of the presence of conspecifics can be two fold. Firstly if competitors observe a cache event, they can steal the food when the cacher has departed from the cache (Bugnyar & Kotrschal 2002). Secondly, through random movement of foraging individuals, food items can also be uncovered without the forager having prior knowledge of the cache. With the latter, group size can be expected to increase the random probability that caches will be uncovered. In the ground squirrels, group size fluctuates daily as individuals move off to prospect at other groups or temporarily disperse. During periods where conspecifics number is low, caching may be more beneficial due to the reduced risk of random cache theft. In **chapter 2**, I therefore predicted that individuals would show sensitivity to the number of conspecifics present and alter their cache decisions accordingly. As this species is a central place forager, a cacher can engage in a number of behaviours to reduce cache loss such as placing items away from a source or at low densities. To test this hypothesis, I provisioned individuals with food items from the centre of their home range to

determine patterns in cache placement. During these observations various measurements such as the GPS coordinates, distance to the centre/nearest individual and the number of individuals present were noted down. I expected that individuals would be sensitive to the number of conspecifics at the time of caching and alter their behaviour accordingly. In addition to behavioural changes at the time of the cache, I also predicted that individuals would change their recovery behaviours in response to differing conspecific number.

In **chapter 3**, I aimed to determine whether cachers took specific cues from conspecifics and altered their decision to cache accordingly. Caching can be a costly behaviour and therefore individuals should be predicted to reduce these costs to increase the benefits from caching food items. As ground squirrels are central place foragers, conspecifics are present throughout the home range, and therefore moving away from these individuals and the centre of the burrow may offer little cache protection. I hypothesised that individuals would not respond purely to the presence or absence of conspecifics, but whether they were attentive to the cache event. Furthermore, I predicted that rank would have an effect on whether individuals chose to cache near conspecifics, due to the variation in competitive ability of individuals of different rank. In responding to this attentive state, cachers would then not have to invest in moving far from the centre of their home range and/or conspecifics where these individuals were naïve to the cache event. For this, I used the data from the observations in chapter 2, but focused on the caches where conspecifics were within 10m of the cache event.

In their paper on foraging in pigs' (*Sus scrofa*), Held et al. (2002), state; "When food finders are exploited by others, but cannot themselves switch to scrounging or leave their foraging group, other behavioural adaptations should be favoured". This exemplifies how an animal can show flexibility in a behavior when they are sensitive to exploitation. In **chapter 4**, I predicted that ground squirrels would show a response to exploitation and exhibit behaviours to counteract this. To identify whether individuals respond to exploitation, I provided a simple choice paradigm of two items with differing payoffs, one item that was always removed when cached and the other that was not disturbed. I predicted that subjects would alter their caching investment in the item that offered reduced reward whilst favouring the item with a higher reward pay off.

Although cache protection strategies can be used to reduce the risk of cache theft, individuals must also balance this with the ability to recover food items. Animals have been shown to use a number of cues in their environment to aid orientation, such as vegetation landmarks (Bednekoff & Russell 1995; Kamil &

Jones 2000) and celestial cues such as the sun (Wiltschko & Balda 1989; Wiltschko et al. 1999). For my final study, **chapter 5**, I predicted that due to the saliency of the sun at the study site that individuals would use this celestial cue when orientating to deposit caches. To test this, I examined movement patterns of individuals when they moved from the source of the food to the cache point and how this movement was related to that position of the sun. I quantified the rules that individuals used in both cache placement and subsequent recovery to determine the degree to which these rules were flexible. As the position of the sun in the sky is constantly changing as the earth rotates, I also tried to identify how these rules changed in relation to these shifts in the sun.

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Chapter 1 (*to be submitted*)

Patterns of caching in a social rodent, the Cape ground squirrel (*Xerus inauris*)

Jamie Samson & Marta B. Manser

Abstract

The caching of food for later consumption is a strategy employed by a number of different animal species for a range of reasons. The decision about when to cache food is driven by many factors, such as resource availability and an individual's hunger or reproductive state. Although classically thought to be a strategy for storing food over harsh periods, this behaviour has also evolved to allow for animals to conceal food from competitors, gain a disproportionate amount of a resource and overcome short-term unpredictability in resource availability. In this study we describe the patterns and properties of caching behaviour within a group living rodent, the Cape ground squirrel (*Xerus inauris*) presenting data on their natural caching behaviour and quantify this in more detail using induced caching events on free-living animals. Caching in this species shows seasonality, occurring just after periods of heavy rains when resources are higher than in drier periods. Besides the effect of abiotic conditions, we show how an individual's sex and age can influence both natural cache patterns and cache site properties. Spatial analysis of caches for this central place foraging rodent suggests that food is dispersed throughout a small area around their central burrow, typical for scatter-hoarding species. Overall this study describes and details how a social living species caches food items and how an individual's caching behaviour is influenced by their age, motivational state and the influence of conspecific group members.

1. Introduction

Caching, i.e. the storing of a resource, occurs in a wide array of animal taxa from birds (for example, Jokinen & Suhonen 1995; Wiltschko et al. 1999; Bugnyar et al. 2007a; Grodzinski & Clayton 2010; Pravosudov et al. 2010), insects (for example, Champion de Crespigny et al. 2001) to mammals (for example, Stapanian & Smith 1978; Hadj-Chikh et al. 1996; Leaver et al. 2007; Zhong et al. 2007; Luo et al. 2014). These species cache food for a variety of reasons (Vander Wall 1990) including in periods when natural stocks are reduced (Pravosudov & Grubb 1997), and protecting food resources from competitors (Balme et al. 2007). As caching has evolved independently in the diverse range of species, there is the suggestion that environmental conditions and behavioural requirements such as the ability to memorise cache location are widespread (Vander Wall 1990).

When to cache and when to eat a food item is an important decision for a foraging animal, where the availability of resources are a key driver of this decision (Vander Wall 1990). In environments where resources fluctuate across temporal periods such as seasons, caching is expected to occur only when the availability of food is high (Willard & Crowell 1965). The build up of such resources can then be utilised over both short periods, ranging from hours to days, and long periods over months (Cowie et al. 1981). The benefits for long-term hoarding is clear, in that animals build up a store of resources which can be potentially utilised over prolonged periods where the general availability of resources is low (Vander Wall 1990). The reasons for short-term hoarding are much less clear, with animals storing and recovering food quickly as food may be perishable (James & Verbeek 1984) or at risk from theft by both con- and hetero-specifics (Heinrich & Pepper 1998). Although all caching species experience loss of some resources due to theft by competitors, social species are expected to experience greater loss due to the constant presence of conspecifics (Hitchcock & Sherry 1995). To overcome this, in some social species caching is undertaken communally, whereby all group members can utilise the same stores (Wolff & Lidicker 1981; Zhong et al. 2007). In social species' where caching is not communal, individuals may benefit from short term storing, by recovering it quickly to reduce the risk of cache loss (Stone & Baker 1989; Fagan et al. 2007). Another way in that caching in a social species can be adaptive, is if individuals steal as many caches as they lose to competitors, in a passive system known as "reciprocal pilferage" (Vander Wall 2003). In systems where individuals are more likely to recover their own caches rather than engaging in this reciprocity, selfish caching may occur (Pravosudov et al. 2010).

Food items can be stored by animals in two general ways, either through scatter-hoarding (for example, fox squirrels, *Sciurus niger,* Stapanian & Smith 1984), where food is stored throughout a given

area, or larder hoarding (for example, Western honey bee, *Apis mellifera,* Seeley 1978) where food is concentrated in a single or few larger stores (Vander Wall 1990). Due to the differences in dispersal of resources with these strategies, the defence of caches differs greatly. In larder hoarders, aggressive defence is usually observed (Preston & Jacobs 2001) as resources are concentrated in one or a few "larders" containing a number of food items. In contrast, in scatter hoarders, where resources are dispersed, aggressive defence is not energetically viable and therefore food is often optimally spaced to reduce complete theft (Stapanian & Smith 1978). When scatter hoarders disperse food throughout a home range, individuals must balance the need to reduce cache loss, whilst maximising the recovering rate and minimising the effort invested in to a cache (Stapanian & Smith 1978; Clarkson et al. 1986). These two types of caching behaviour are not dichotomous in some species, where there is a flexible shift between the two strategies (Jenkins et al. 1995; White & Geluso 2012). For example, in Ord's kangaroo rats (*Dipodomys ordii*), a shift from scatter to larder hoarding occurred during winter time where this species uses a single burrow and therefore making it easier to defend a central store (White & Geluso 2012).

Individuals within species vary in their behaviour, where sex differences may be a result of divergent life-history strategies (Burns & Steer 2006) and age differences may be due to experience (Beach & Jaynes 1954). Some studies, indicate that differences in caching behaviour between sexes is due to the social dominance of one sex over the other, such as in New Zealand robins (*Petroica australis*, Burns & Steer 2006). Alternatively, a number of studies have shown that differences in caching behaviour could arise through variations in energetic needs (McLean & Towns 1981; Miceli & Malsbury 1982; Vander Wall 1990). Females are often the sex that stores at higher intensities and this could occur in response to the need to acquire resources during reproductive periods (McLean & Towns 1981; Vander Wall 1990). Female Ord kangaroo rats, for example, increase their larder hoarding rates in the summer, possibly to increase their energy sequestration in the breeding period (White & Geluso 2012). The effect of age has been understudied in relation to caching behaviour, with conflicting results. For example yearling willow tits (*Parus montanus*) cache at higher intensities than adults (Lahti & Rytkonen 1996), whereas in related species yearlings and adults cache at similar intensities (Coal tit, *Parus ater,* Brotons 2000), or adults cache at higher intensities (Crested tit, *Lophophanes cristatus,* Lens et al. 1994).

Cape ground squirrels (*Xerus inauris*) are medium sized (at maturity 500-700g) rodents that inhabit arid areas of Southern Africa, ranging from Botswana and Namibia and down in to South Africa (Waterman 1995, Waterman 1996, Hillegass et al. 2008). This species can live in groups of up to 19 individuals, that

typically consist of 1-3 reproductively active adult females, subadults/juveniles and pups of either sex (Hillegass et al. 2008). Males disperse at around 16 months, but may delay this, staying within their natal group and being reproductively active within this group until they are 1-2 years of age (JS personal observation). Groups of males may form coalitions with a large territory size often encompassing a number of groups (Waterman 1997). These males prospect around this range but normally sleep independently of the mixed groups (Waterman 1997). At the site of this study, ground squirrels form mixed groups where both adult males and females interact and sleep in the same burrow system (JS unpublished data).

In this study, we describe our observations on the natural caching patterns and on induced caching in the Cape ground squirrel. Firstly, we examine the temporal patterns of natural caching and its relationship to abiotic conditions, and secondly, we explore the variations in caching rates between the sexes and age categories. As this species home range habitat shows seasonality, we predicted caching would show fluctuations throughout the year, in response to changing climatic conditions and resource availability. Due to life history variations amongst sexes and age categories, we hypothesised that caching behaviours would differ amongst these demographic groups. We used observations in which we provisioned adult subjects with food from a central location to explore cache dispersal, the type of cache individuals made (such as a false caching, Steele et al. 2008) and the properties (such as cache depth) of these caches. Here we predicted that subjects would disperse caches at short distances from their home burrow and that the type of cache a subject makes will affect the properties of that cache.

2. General materials and methods

Study species and study site

The study was conducted at the Kalahari Ground Squirrel Project, Kuruman River Reserve, in the Northern Cape, South Africa. Cape ground squirrels occurred readily at this site, with groups concentrated mainly along the dry Kuruman riverbed, where vegetation is denser than in the surrounding areas. All individuals in the population were uniquely marked with hair dye (Garnier, L'Oreal, UK), to allow for individual recognition. Due to large testes in males, all individuals were easily sexed and where full life history had been recorded (21/51 individuals), an individual's exact age was known. Where age was not known, we estimated an individuals age class based on weight and visual appearance. Individuals were assigned in to four age classes; pup (0-3 months), juvenile (3-6 months), sub-adults (6-12 months) and adults (>12 months).

Statistical analysis

All statistical analyses were performed in R; release GUI, version 3.2.0 (R Core Team 2015). Linear mixed models (LMM) were used throughout, as these allowed for the inclusion of random effects. For the all models from the natural observations, we included year as a random effect. For observations on induced caching all models contained trial as a random effect to control for repeated measures. To determine the overall effect of a factor, we used likelihood ratio tests (here after LRT, χ) to compare models with the factors (or interaction of factors) included and excluded (Crawley 2007). In all models, variance components were estimated using maximum likelihood ("ML") methods and additionally all random effects were kept in the models. As all model outputs only gave us the comparisons to the intercept, post-hoc multiple comparison tests with manually assigned contrasts were run to examine the differences between all factor levels in the models ("multcomp" package, Hothorn et al. 2008).

a. Natural caching patterns

Material and methods

Observational procedures

All data analysed in this study were from a long-term project (May 2011-June 2015), on 10 groups of free-living Cape ground squirrels. Caching observations were analysed from *ad libitum* sampling, where we observed groups for 90 minutes from 15 minutes after they emerged in the morning and for 60 minutes before they went below in to their burrow for the night. Two morning and two evening sampling sessions were conducted at each group per week by a number of different observers. During this sampling, we collected data on handheld computers (Palm TX Tungsten, Palm Inc, 2005) using Cybertracker software (Cybertracker Conservation, 2013) to record the behaviours.

Weather data

Meteorological data was collected on a weather station (UT10 Weather Station, Campbell Scientific Inc, 1993-2010) located on the reserve, which recorded amongst other things, minimum and maximum daily temperature (^{o}C) and 24-hour rainfall measurements (mm). For this study, mean daily temperature and total

daily rainfall was used. For temperature measurements, this data was averaged over each monthly period and for rainfall data, the total amount of rain per month was calculated.

Results and discussion

Temporal patterns

The rate of caching was examined across monthly periods from January 2012 – June 2015. Caching occurred throughout the year, with a mean monthly caching rate of 0.06 ± 0.04 (mean ± SD) caches/hour. Comparing the rate of caching across months to probabilistic uniform distribution showed that caching rates were not uniformly distributed (Kolmogorov-Smirnov test, D = 1, $p < 0.001$). There was an overall effect of month on the rate of caching that occurred (LRT, $v_1^2 = 26.52$, $p = 0.005$), with peaks in caching in April (LMM comparing rate to overall mean, $t = 2.91$, $p = 0.005$) and May (LMM, $t = 3.08$, $p = 0.003$). Neither temperature (LRT, $v_1^2 = 2.36$, $p = 0.125$) or rainfall (LRT, $v_1^2 = 0.02$, $p = 0.890$) had any effect on the rate of caching, although the peaks in caching occurred after the peak in rainfall in March. These peaks in caching intensity, however, occurred just after the heaviest bouts of rainfall, which suggests that caching may be linked to the availability of food (Willard & Crowell 1965; Vander Wall 1990). As vegetation growth shows a lag from rainfall events, resources will only start to become abundant after a delay (Porporato et al. 2003), when the sand has become saturated. As caching still occurred throughout the year, but at lower intensities than the peak months, caching in this form may occur where animals have become satiated and caching serves to store a resource when availability is unpredictable (Lucas et al. 1993).

Demographic differences

Female squirrels (0.05 ± 0.06 caches/hour) cached at the same rates as males (0.03 ± 0.04 caches/hour, LRT, $v_1^2 = 3.048$, $p = 0.081$, Figure 2a.), although there was a tendency for females to cache at higher rates. Sex differences in caching rates have been suggested to arise due to different energetic needs, where reproductively active females need to acquire substantial resources during pregnancy and lactating periods due to the nutritional demand of offspring (McLean & Towns 1981; Vander Wall 1990).

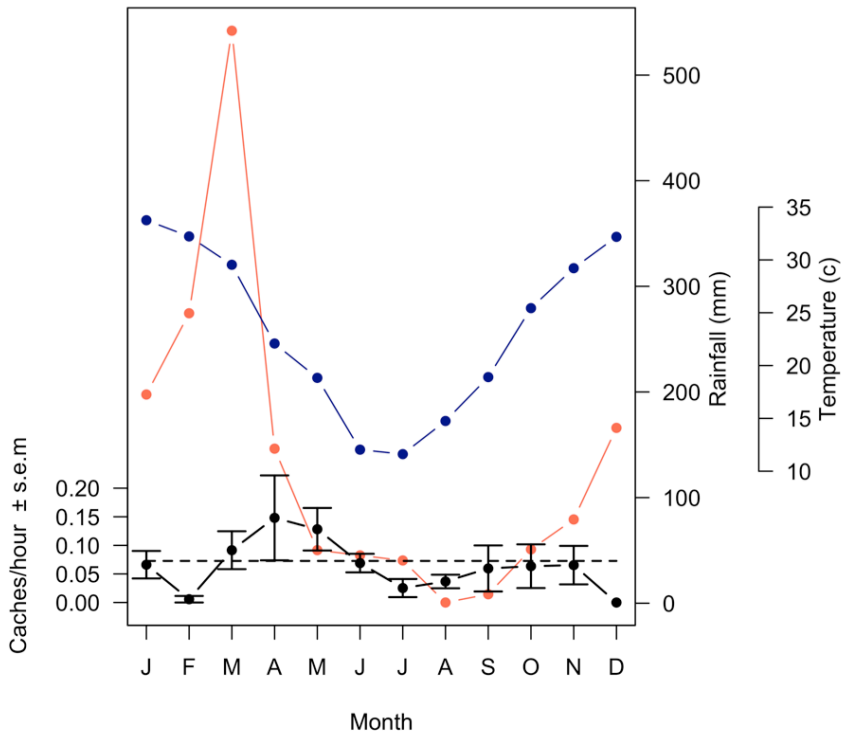

Figure 1: Temporal patterns in caching across monthly periods (black solid line) with the overall mean caching rate shown as the black dotted line (the vertical bars refer to the mean ± se). Mean monthly temperature (blue) and total monthly rainfall (red) are represented on the secondary axis (y_2).

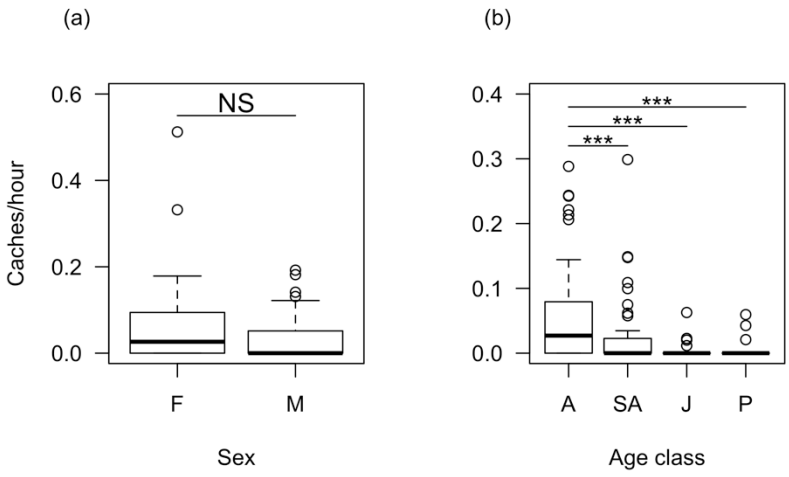

Figure 2: Differences in the rate of caching between (a) sexes (F= females, M= males), and (b) age classes (A = adult > 12 months, SA = sub-adult: 6 – 12 months, J = juvenile: 3 – 6 months and P = pup < 3 months).

The monthly rate at which reproductively active females (> 12 months of age) cached food was not related to the number of births within that month (LRT, v_1^2 = 0.803, p = 0.370). As female squirrels show all year round breeding (JS unpublished data) and caching appeared to show some seasonality, caching may not be

beneficial in low resource periods and therefore instead food is consumed upon discovery. Comparing age classes, we found that adults cached at higher rates than sub-adults (LMM, t = -4.21, p < 0.001), juveniles (LMM, t = -7.38, p < 0.001) and pups (LMM, t = -7.52, p < 0.001, Figure 2b.). Overall, there was a linear increase in the caching rate across age categories from pups to adults (LRT, v_1^2 = 50.13, p < 0.001). These age differences in caching behaviour could haven arisen through the ability of animals to store and retrieve cached food with more experience or maturation (Sechley et al. 2014), or through age related effects on foraging efficiency (Loman 1984). For example older female grey jays (*Perisoreus canadensis*) are more efficient at storing and recovering food, which is suggested to have a positive impact on their weight gain during reproductive periods and lead to better breeding condition (Sechley et al. 2014).

b. Induced caching

Materials and methods

As natural caching events will be influenced by a number of confounding factors, we induced caching by provisioning food to allow us to examine caching in a more controlled way. Observations were collected from March - June 2013 during the afternoon, which coincided with the highest periods of caching (16:30-19:00 P.M.; JS personal observation). Observations were undertaken on adult individuals only (N = 14; group 1 = 3 males and 2 females, group 2 = 2 males and 3 females, group 3 = 3 males and 1 female) for 30 minutes, during which time animals were followed throughout. Observations were repeated six times for each individual across separate days; however, for 2 individuals a full set of repeats could not be achieved due to emigration of these individuals out of the groups. Therefore, over the course of the study, 69 observation sessions (group 1 = 22, group 2 = 28, group 3 = 19) were undertaken with 377 induced cache events recorded.

During trials individuals were provisioned with standardised food items to cache (25 ± 0.25 mm size peanuts in the shell), to control for variation in behaviour due to items differing in quality (Preston & Jacobs 2009). All items were provisioned to the individuals from the centre of the home range to control for variations in distance moved at differing provisioning points. When an animal cached a food item, the point was recorded using a Garmin GPS MAP62 handheld GPS device (Garmin LTD, 1996-2013). In addition the location of an item in relation to landmarks was recorded, where caches placed near landmarks had to be made so within 1 m of either a permanent habitat feature such as a shrub or a temporary feature such as

angiosperms or a patch of grass. When an individual took an item to cache, we noted down the caching behaviour type, either as "true", "null" or "false". A true cache was defined as when an individual buried an item, covered it and moved away, whereas a "null cache" referred to when a hole was dug, but the individual moved off without re-covering the hole or placing the item inside the dug hole. False caching (Steele et al. 2008) referred to where a hole was dug, the food item placed inside and the food item removed before the hole was covered and the squirrel moved off to cache elsewhere. During these false caches, a nearby conspecific often approached the hole and examined it, often putting their head in the hole and digging for 1-2 seconds before moving off (JS personal observation). To determine the properties of caches, caching locations were marked with sand coloured non-descript tokens and when the squirrels had moved below ground for the night the observers revisited the caches to take measurements. The cache diameter referred to the greatest distance between edges of disturbed surface sand left when a hole was re-covered. The cache depth was the deepest depth of the cache hole, determined from the depth of the loose sand caused by the digging action of the squirrel.

To determine whether caches were placed near landmarks, we calculated the number of caches that would be expected to be placed near a landmark and compared this to the observed number. This expected number of caches was determined by calculating the total caching area for each for group and within this area the percentage covered by landmarks (m^2). This then allowed us to calculate the number of caches we would expect to be placed within 1 m of landmarks if caching occurred randomly throughout the total caching area. For the spatial distribution of caches, we used the 'envelope' function in the "spatstat" package in R (Baddeley & Turner 2005) to calculate whether the distribution of caches showed complete spatial randomness (hereafter, CSR). The CSR models were simulated (n = 100) and the results plotted which showed whether our observed data fitted the theoretical null hypothesis that there was complete spatial randomness, i.e. homogeneity of caches within a given cache area.

Results and discussion

Cache properties

The distribution of distances, from where the caches were placed from the provisioning point, described a distribution not statistically different from a probabilistic normal distribution (Kolomogrov-Sminov test: group 1, D = 1.00, p = 0.292; group 2, D = 1.00, p = 0.289; group 3, D = 1.00, p = 0.105; Figure 3a.). The

distances caches were placed from the burrow may suggest that individuals cached in optimal locations that may balance the trade off between costs in terms of energy expended and benefits in terms of cache recovery (Stapanian & Smith 1978; Clarkson 1986). Cache recovery in this instance relates to the likelihood a cache is uncovered by a competitor (Hopewell & Leaver 2008). The distribution of caches identifies that this species shows scatter hoarding tendencies (Figure 3b.), however within each groups caching area, caches were not homogenously distributed (Figure 3c.).

During observations, individuals moved on average 17.02 ± 13.92 m away from the source to bury the food, digging holes of 11.71 ± 3.07 cm in diameter and 4.25 ± 1.04 cm deep (for true caches unless stated). No sex differences were found in the diameter (LRT, $v_1^2 = 0.01$, p = 0.918) or depth (LRT, $v_1^2 = 0.23$, p = 0.631) of caches, but there was a tendency for females (mean distance from source = 32.33 ± 15.74 m) to move further from the source than males (25.54 ± 9.42 m, LRT, $v_1^2 = 3.34$, p = 0.068). The similarities between the sexes in these cache properties may be driven by the need to cache at optimal distances and depth that reduce energy expenditure and cache loss.

Cache placement

Of the 377 events observed in these trials, 116 caches were made within 1 m of a landmark (proportion test: caches placed near landmark: total caches, $\chi^2 = 55.00$, $p < 0.001$). We found that caches were more likely to be placed within 1 m of landmarks than would be expected by chance given the level of landmark coverage within the caching area of the groups (Paired t-test, T = -4.85, df = 14, $p < 0.001$, Figure 4). Caching near landmarks may allow for more efficient recovery of food items, as habitat features will provide a frame of reference directing the animal back to the cache (Vander Wall 1982; Kamil & Cheng 2001; Bruck & Mateo 2010). At the study site, vegetation is sparsely distributed and where vegetation is absent the landscape is featureless, with flat sand plains, which will reduce the ability of an animal to re-orientate back to a cache site.

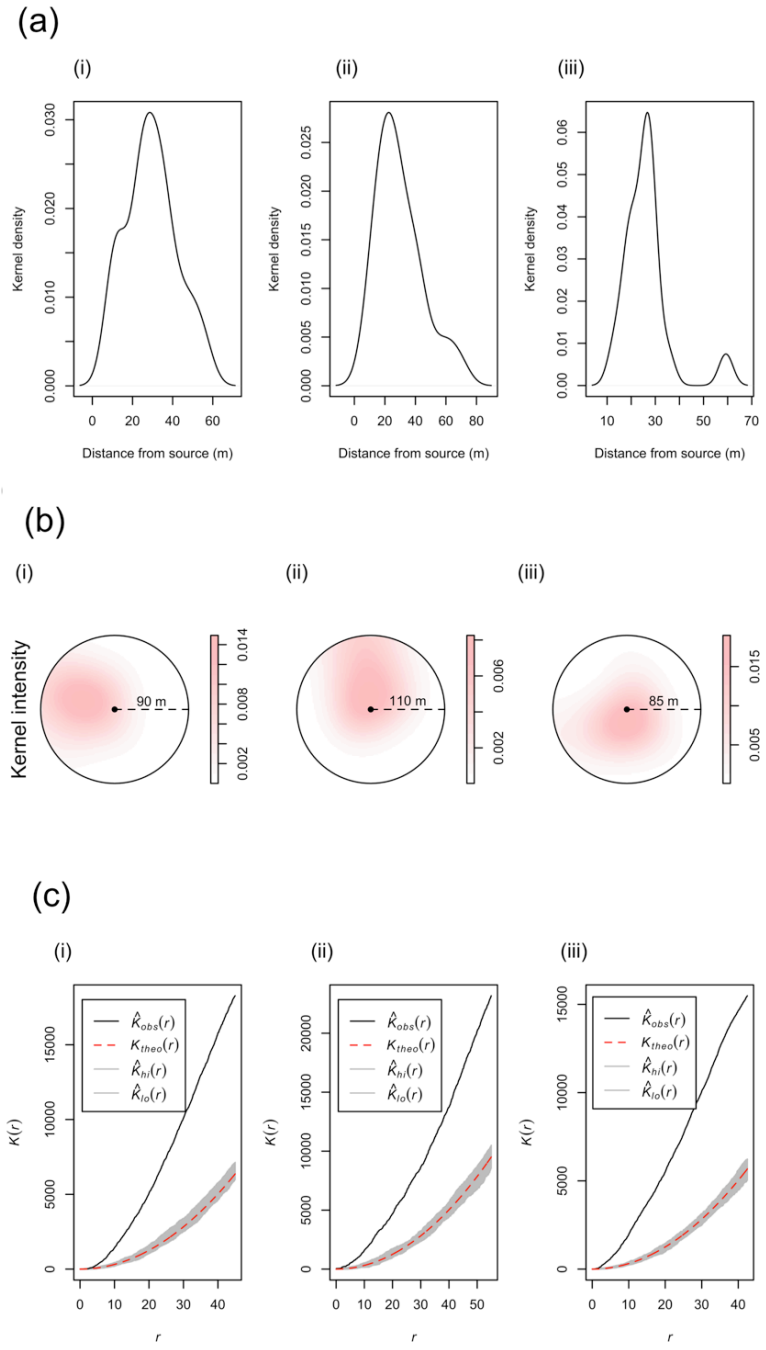

Figure 3: Kernel density plots of the distances from the source to the cache site for each of the 3 groups used (a). Kernel smoothed intensity function plots for the distribution of caches (b). The radius (dashed line) refers to the distance between the centre of the group's home range and the furthest point a cache was recorded (hereafter referred to as caching range). The distribution of caches within the caching range was tested to determine if it described CSR (c). The divergence of the observed line (black solid) from the theoretical (red dashed) suggests caches are not homogenously distributed throughout the caching range, but rather show some clustering.

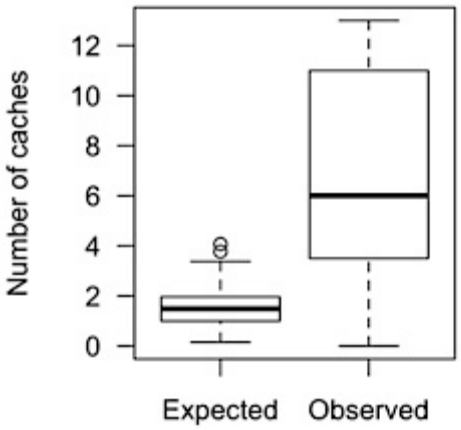

Figure 4: The number of observed and expected caches placed within 1 m of a landmark.

Cache type

Of the 156 caches where the depth and diameter were recorded, 116 were true caches, 30 null caches and 10 were false caches. There was an overall effect of cache type on cache diameter (LRT, v_1^2 = 14.08, p < 0.001), with true (11.77 ± 3.08 cm) and false (9.33 ± 1.62 cm) caches showing similar diameters (LMM, t = -1.43, p = 0.158), but null caches were wider than true caches (LMM, t = -3.80, p < 0.001). Both null and false caches had similar diameters (LMM, t = 1.94, p = 0.123). Overall, cache depth differed between the cache types (LRT, v_1^2 = 44.35, p < 0.001), with null caches (null cache depth = 3.23 ± 0.86 cm) being shallower than true caches (true cache depth = 4.46 ± 1.09 cm, LMM, t = -5.218, p < 0.001) and false caches being deeper than true caches (false cache depth = 6.15 ± 2.27 cm, LMM, t = 4.37, p < 0.001). In addition, false caches were deeper than null caches (LMM, t = 6.87, p < 0.001). Cache type appears to influence the diameter and depth of caches, which suggests that individuals actively alter these properties when storing food to reflect cache type. True caches need to be deep enough to minimise the risk of theft if food is visible on the surface in the cache hole but as the ground becomes hard below the oxidised topsoil, individuals will expend more energy digging deeper holes in to the subsoil layers. Therefore the depth of true holes may be a trade off between reducing theft and reducing the energy expended in digging the hole. The depth of the false holes may be linked to the behaviour of conspecifics, whereby when a competitor submerges their head in the false hole, the cacher has time to move off and place the food elsewhere.

3. General discussion

The results from this study on the Cape ground squirrels describe in detail the patterns of caching behaviour in a free-living social rodent species. Caching appeared to be seasonal in this species, with peaks occurring just after the highest periods of rainfall between March-April. Although both sexes cached at equal rates, there appeared to be a strong affect of age on the rate at which food was cached. Through observations on induced caching behaviour we were able to show the spatial distribution of caches and how properties of the holes dug during caches events varied with cache type. Altogether this study highlights how environmental, ontogenetic and social cues may have impacted on the caching patterns observed in this species.

In the Cape ground squirrels, as caching appeared to increase after the heaviest periods of rain, this behaviour may be linked to the availability of resources (Willard & Crowell 1965). Where an animal lives in a highly competitive environment such as a social group where habitat resources are ephemeral, caching allows an individual to conceal resources which otherwise might become quickly depleted (Balda & Bateman 1971; Dally et al. 2006). Due to the aridity of the habitat this species occupies, resource availability for much of the year may be too low for caching to be viable. This aridity could account for why we observed no sex differences related to reproductive costs in cache intensities, as due to the need for females to sequester energy during reproduction, food may be consumed instead of cached. Unlike other studies highlighting sex differences (McLean & Towns 1981; Vander Wall 1990; White & Geluso 2012), due to the sociality of this species and therefore the risk of theft, caching may be maladaptive in females as a means of securing energy reserves whilst pregnant. Caching as a foraging strategy appears to be influenced by the age of the individual, where older individuals may learn the potential value of caching food items (Clayton 1992; Bugnyar et al. 2007b). In marsh tits (*Parus palustris*) for example, caching may be an innate behaviour, where social learning is not needed to initiate caching (Clayton 1992). However, caching appears to improve with age in marsh tits, where the appropriateness of food items and caching intensities increases with age. An alternate hypothesis proposed is that the high cost of caching and high predation risk may impact on the amount of food non-adults can cache (Lens et al. 1994). In our example as caches were made on average 17.02 m from the burrow, this distance will not be of high cost to foraging individuals and all individuals who reach independence can be assumed to be under the same predation pressures.

As caches appeared to be dispersed throughout a home range, Cape ground squirrels showed strong scatter-hoarding tendencies. As this species does not communally cache, scatter hoarding is a more viable technique than larder hoarding, as aggressive defence is not feasible in large social groups (Grant 1993). Due

to the degree of scattering exhibited by individuals, complete pilferage of food from all cache sites seems unlikely and therefore this strategy may decrease the likelihood that caches are stolen and instead rather recovered by the cacher (Stapanian & Smith 1978; Clarkson et al. 1986). Although the dispersal of caches were done throughout a defined area (Stapanian & Smith 1984), caches were not homogenously dispersed in this given area but there was some clustering around the central sleeping burrow. As no homogeneity was observed and caches were placed at a short distance from the burrow, food may be being placed in optimal locations that may increase the likelihood a resource is recovered whilst decreasing the chance of it getting stolen (Stapanian & Smith 1978; Clarkson et al. 1986). In addition to the spatial patterns of caching, individuals also favoured cache sites near landmarks in which to deposit food. These two features together may highlight ways in which individuals can maximise the recovery advantage of a stored food, by storing in locations which reduce complete cache loss to competitors but also allow for successful recovery utilising habitat landmarks (Vander Wall 2003).

This study highlights the temporal and spatial caching patterns of a social species inhabiting an arid environment. Caching can provide a means by which animals store resources for later consumption, and the drivers of this behaviour, such as an increase in availability of food can vary widely across temporal scales. In addition to such seasonal effects, we have shown how demography, life history and social environment can also influence caching behaviours.

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Chapter 2 (*to be submitted*)

Group size effects on cache survivability and decision-making in the Cape ground squirrel (*Xerus inauris*)

Jamie Samson, Jobran Chebib & Marta B. Manser

Abstract

Caching has evolved in a number of different species to ensure food availability when stocks are low or unpredictable. In these species, many studies have shown how individuals can evolve various strategies, to increase the survival of stored food and limit theft by competitors. The influence of competitors on cache survival can occur in two distinct ways, either through immediate theft of a food item or delayed theft after the cacher has departed. In social species, both of these categories of cache theft will be influenced by conspecific competitor behaviour, but in distinct ways. In this study, we examined how the social environment in the group living Cape ground squirrel (*Xerus inauris*) affected caching decisions and survival of cached food, focusing on delayed cache loss. We found that an increase in the number of individuals in a group caused a reduction in the survival times of food stores. Using an agent based model we show that increasing the number of individuals in a parameter space decreased the time it took for a randomly placed cache to be uncovered. Cachers did not alter either the distance from their central burrow or the density at which caches were placed in response to varying competitor number. Applying theoretical approaches to our empirical data, we argue individuals are caching at optimal distances and densities around their burrows rather than changing cache locations in response to competitors. However, we did find that individuals reduced the proportion of provisioned food they cached, but any food that was cached was not recovered more quickly when competitor number was high. This study highlights how a species can show a flexible response to varying social conditions to ensure the benefits from resources are optimised.

1. Introduction

There are various benefits such as predator protection (Clayton 1978) and costs such as increased competition (Rubenstein 1978) to animals living in social groups. Where resources are limited, competition for access to these are expected to increase with an increase in group size (Beauchamp & Fernandez-Juricic 2005). Therefore, we can predict that individuals may try to alleviate competition by engaging in behaviours that maximise their own needs (Frank 1995) whilst reducing loss to conspecific competitors. For example, black-capped chickadees (*Poecile gambeli*) alter their food caching behaviour in response to the presence of conspecific group members, but not when competitors are absent (Pravosudov et al. 2010). Although, caching may seem maladaptive in social living species due to the continual presence of competitors, a large number of caching species are social living (Ekman et al. 1996; Dally et al. 2005; Toomey et al. 2007; Pravosudov et al. 2010; Samson & Manser 2015).

All species that cache experience loss in some form or another, whether it is from competitors (Hopewell & Leaver 2008), the food item degrades in the cache site (Janzen 1977; Vander Wall 1990) or individuals do not recover items they cache (Vander Wall 1990). In some species, no behavioural changes are observed when competitors pilfer caches, as these individuals may learn to accept a certain level of cache loss (Vander Wall 2003). This is known as the "pilferage tolerance strategy" (Vander Wall 2003), but far from being passive in their behaviour, individuals who engage in this strategy might increase the rate at which they pilferer caches to compensate for this loss of their own caches (Vander Wall 2003; Zhang et al. 2011). The alternate strategy is "pilferage avoidance", in which animals try to reduce theft from their caches by employing a range of counter-strategies (for a review see Dally et al. 2006) such as being sensitive to audience attentiveness (Samson & Manser 2015), behavioural deception (Steele et al. 2008) and re-caching behaviours (Emery et al. 2004). In social species where competitors are always present, cache loss may be higher than in solitary species (Vander Wall 1990) and therefore a low level of loss may be accepted (Vander Wall 2003). However, these species may also engage in cache protection strategies so that the loss of caches does not exceed the benefits from recovering food items (Preston & Jacobs 2001). Animals may benefit from flexible decision-making when caching in variable social contexts, so that they can maximise the energetic gains from resources (Andersson & Krebs 1978), only responding where there is high potential for cache theft. For example, Cape ground squirrels (*Xerus inauris*) do not just respond to the presence/absence of conspecifics, but they alter their behaviour where individuals are attentive to the cache event (Samson & Manser 2015).

Even when individuals employ cache protection strategies, cache loss will be expected to occur due to the random foraging movements of competitors in a given area (Stapanian & Smith 1978; Clarkson et al. 1986; Stone & Baker 1989). Studies have highlighted that where cache loss does occur, individuals engage in a number of different strategies, such as ceasing caching (e.g. Willow tits, *Parus montanu*: Lahti & Rytkonen 1996) to increasing their caching effort (e.g. Eurasian jay, *Garrulus glandarius*: Bossema 1979). Where caching still occurs it will only expected to be adaptive where the benefits from recovering an item outweighs the investment in caching that item (Andersson & Krebs 1978; Stapanian & Smith 1978; Hopewell et al. 2008). Therefore, when items are cached, individuals must do so at optimal locations (Stapanian & Smith 1978; Waite 1988) to maximise net benefits whilst reducing net loss. In their model of scatter hoarding patterns, Stapanian and Smith (1978) highlight the importance for an animal to balance the distance and density of caches around a central source. They argue that individuals must cache at locations that reduce the potential for thieves to uncover caches (and successive caches), but also not so hyper-dispersed that the cost of recovering outweighs the benefits.

In this study we examined how Cape ground squirrels altered their caching behaviour in response to fluctuations in the number of conspecific competitors. This species is a highly social rodent (Waterman 1995) living in groups of up to 36 individuals (largest group at the study site, JS personal observation). Cape ground squirrels are scatter hoarders, placing items around their central burrow (Samson & Manser 2015) in small shallow caches. Caching occurs all year round, with peaks at the start of the winter months (May - July) and a decline in the early summer (December - January). Recovery usually occurs within 24 hours of a cache being made, which maybe be related to the risk of theft by competitor group members (JS unpublished data). Due to their sociality, we predicted that individuals would be sensitive to the presence of competitors and that they would change their behaviour to reduce the risk of cache theft. We expected that individuals would engage in a number of different cache protection behaviours with increased number of competitors close by, such as (1) caching at low densities and at greater distances from their burrow (Stapanian & Smith 1978; Clarkson et al. 1986), (2) reducing the amount that they cached (Carrascal & Moreno 1993) and (3) recovering items more quickly (Brodin 1992).

2. Methods

Study site and study subjects

The study was conducted at the Kalahari Ground Squirrel Project, Kuruman River Reserve, in the Northern Cape, South Africa. The reserve is classified as "green Kalahari", where sparsely vegetated dunes are interspersed with more vegetated flat plains (see Brotherton 2001; Russell et al. 2002 for further details). Cape ground squirrels occured readily at the study site, with groups concentrated mainly along the dry Kuruman riverbed, where vegetation is denser. We collected data on three mixed sex groups ("HE", "IC" and "WK") of squirrels that were habituated to close human observation. All individuals in these groups were sexed and uniquely marked using coloured hair dye (Garnier, L'Oreal, UK). Dominance ranks for individuals in groups were calculated using David's scores (De Vries et al. 2006) which were ascertained from socio-matrices of antagonistic interactions. Groups were then split in to three categories; high, medium and low rank classes (number of individuals in each category in this study, high = 7, medium = 3, low = 4).

Observational procedures

Observations were collected from March - June 2013 during the afternoon, which coincided with the highest periods of caching (16:30 - 19:00 P.M.; JS personal observation). Focal data on caching behaviour were undertaken on individuals (N=14; HE = 3 males and 2 females, IC = 2 males and 3 females, WK = 3 males and 1 female) for 30 minutes, during which time animals were followed throughout. Observations were repeated six times for each individual across separate days; however, for two individuals a full set of repeats could not be achieved due to emigration of these individuals out of the groups (69 observation sessions, HE = 22, IC = 28, WK = 19). Individuals were provisioned with food items (mean ± SD, 25 ± 0.25 mm size standardised peanuts in the shell) from the centre of the groups' burrow system (hereafter, source). As this species is a central place forager this centre point also refers to the centre of the home range of that group. When the animals moved from the provisioning point to the cache points, we recorded two behaviours, how vigilant the caching individuals were and whether items were re-cached. Vigilance scans were defined as when a caching individual paused its movement and looked around or got up on to its hind legs. We recorded the absolute number of scans and in addition divided this by the distances moved from the provisioning point to the cache point to calculate the number of scans as a product of distance. Re-caching behaviours occurred when an individual dug a hole and placed an item inside, but then removed the item and cached elsewhere. We also recorded the attentive behaviour of conspecifics nearby to the cacher (within 10m, Samson & Manser 2015) so that this could be controlled for in our analysis.

Cache survivability

To determine whether caches were stolen by conspecifics or recovered by the cacher, we examined the fates of caches (n = 38) by setting up remote cameras (5210A series, LTL-Acorn Outdoors) near the site for five days and recording 15-second videos whenever the infrared component was triggered (see also Samson & Manser 2015). To determine the lag time in caching to the theft/recovery event, we used the potential foraging hours between the two time points. As we recorded the time individuals went below in to their burrows for the night and the time when they got up in the morning, we used the periods in which they were active as the potential foraging hours (as they tended to forage as soon as they got up and stopped foraging just before they went below in the evening, JS personal observation).

We built simulation models to test how varying numbers of individuals can affect the likelihood and speed at which food items were removed (Van Rossum 2000). Agents (n = 1 to 20) were allowed to perform random walks (n = 2000 repeats per number of individuals) from a centre point within the parameter space (analogous to the caching area). For each simulation an item was placed in a random location within the parameter space. These walks consisted of a maximum of 100 discrete steps, after which the simulation was stopped. If an agent uncovered an item before 100 steps, the simulation ceased and the step number was extracted. Although a parameter space was defined, agents could move freely in and out of this area.

Determination of distance from source and nearest neighbour distance

A Garmin GPS MAP62 handheld GPS device (Garmin LTD, 1996 - 2013, radial standard accuracy of ± 1.5 m) was used to record the coordinates of the caches and Garmin Basecamp (Garmin LTD, 1996 - 2013) was used to import the data. To calculate the distance from the source, all coordinates were converted to UTM using the "move" package in R (Kranstauber et al. 2013) and then the linear distance between the source and cache points was calculated. To determine the nearest neighbour distances (hereafter, NND), we used the 'nnd' function in the "spatstat" package in R (Baddeley & Turner 2005), calculating the distances within observational periods.

Caching range size

To determine the home range of groups (i.e. the foraging patch) we used the long-term data from the study population. Individuals were either focal sampled across a whole day from an hour and a half after they had emerged and went below for the night, or for 30 minutes in the morning an hour and a half after they had emerged in the morning. During the focals, GPS coordinates were collected every 15 minutes, or were

collected more frequently if the individuals made significant movements (>10 m). We used all of the coordinates to calculate the 95% convex hulls of the home range using the "dismo" package in R (Hijmans & Elith 2015). This was done to ascertain the general area encompassed by foraging animals and link this to where caches were placed. As we were not concerned with the movement patterns of foraging animals, only the home range, we could combine the focal types.

Determination of optimal cache distance and NND

To determine within trial optimum distances from source and NND's, we used the model developed by (Stapanian & Smith 1978);

$$\overline{D} = D^{max}/\sqrt{2}$$

Where $\overline{D}$ is the average distance (within a trial) and D^{max} is the maximum distance (within a trial) of caches. This model predicts the average distance at which caches should be placed given a maximum cache distance. This maximum distance is assumed to refer to the point at which the costs equal the benefits of caching. One of the assumptions of the model is that an optimum distance/density is maintained; otherwise the costs and benefits will vary for each successive food item. Although optimum distances/densities in this study were not determined, the distance from source and NND were constant within trial observations (distance from source: LRT, v_1^2 = 3.27, p = 0.070, NND: LRT, v_1^2 = 0.67, p = 0.415). This allows us to use this equation, whereby the constancy of the distance from source and the NND act as the optimum. We used Stapanian & Smith (1978) model of cache placement as opposed to the model of Clarkson et al. (1986) as the distance from the source nor the density of caches affected cache loss and these distance or densities were not affected by the order of food presentation (JS unpublished data).

Statistical analysis

All statistical analyses were performed in R; release GUI, version 3.2.0 (R Core Team 2015). To determine differences in group size across the study period we used general linear models, with the number of individuals as the response variable and the group as an explanatory variable. To identify whether the number of individuals in the groups changed over time, autoregressive integrated moving average (ARIMA) models were run on each of the groups and then tested using Ljung-Box statistics (Chan & Ripley 2012). For the data concerning cache survivability, linear mixed models (Bates et al. 2014) were used, where the response variable was time to theft/recovery and the number of individuals present as the explanatory variable.

Individual ID (of the cacher) nested within group was assigned as a random effect to control for the variation within these factors. For the simulations of cache survivability, linear models were used for the number of steps and a general linear model with a binomial error distribution (Crawley 2007) was used to examine their relationship with the number of agents (individuals). Linear mixed models were also used to compare the distance from source and the NND with the theoretical values obtained from (Stapanian & Smith 1978) model, where individual ID nested in group and trial number (to control for repeated measures) were assigned as random effects. To establish how the proportion of items cached to consumed changed with the number of individuals present, we used a generalised linear mixed model with a binomial error structure, with individual ID nested within group and trial number as random effects. In determining how the behaviour of the animals when moving to cache was effect by the number of conspecific present, individual ID nested within group and trial number as random effects. For the various distances, cache proportions and behavioural models, whether audience members were attentive to the cache was additionally assigned as a random factor, as this has been shown to affect caching behaviour (Samson & Manser 2015). In all models, variance components were estimated using maximum likelihood ("ML") methods and additionally all random effects were kept in the models. The significance of explanatory variables for all models (both general linear and mixed models), were determined using likelihood ratio tests (hereafter, LRT, Crawley 2007), whereby models with these variables were compared to models with the variables removed. Kolmogorov-Smirnov tests (hereafter, KS-test) were used to compare the distributions of the distances from source or NND with that of probabilistic normal distributions ("pnorm" base function in R).

3.Results

Differences in group size

There was an overall difference in size between the groups studied (LRT, v_1^2 = -12.44, p = 0.002), with WK (hereafter, mean ± SD, 11.08 ± 2.96) containing on average more individuals than HE (7.38 ± 3.03, GLM: z = -3.276, p = 0.003) and IC (8.14 ± 4.02, GLM: z = -2.721, p = 0.018), with the latter two groups being of similar size (GLM: z = -0.828, p = 0.686). We found that in all groups the number of individuals randomly fluctuated across days and were not temporally correlated with the previous days total (Ljung–Box test: HE: χ^2 = 4.52, p = 0.150, IC: χ^2 = 6.17, p = 0.800, WK: χ^2 = 17.78, p = 0.059).

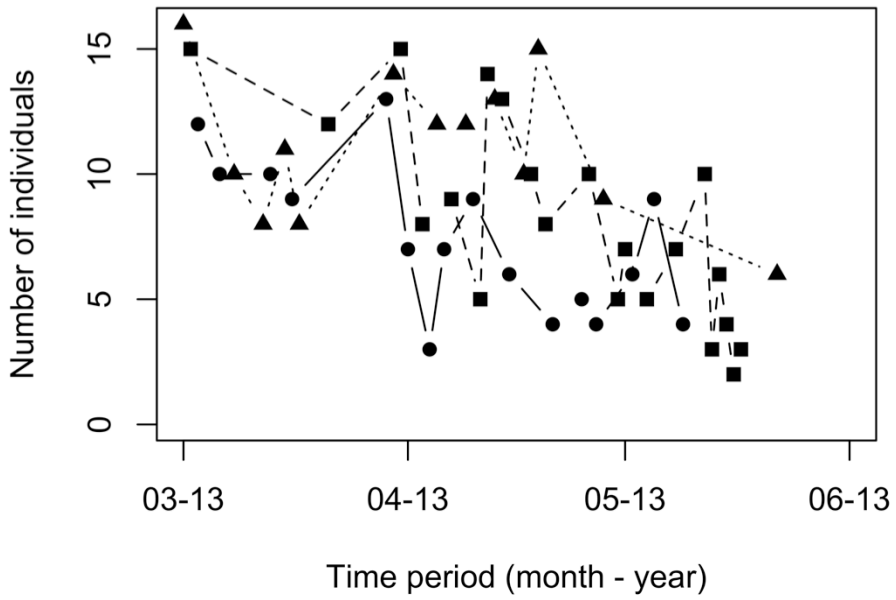

Figure 1: Fluctuation of total number of individuals present within the groups across the time period of this study (HE solid line and circles, IC dashed line and squares, WK dotted line and triangles).

Cache survivability and group size

During the period of the study, 55.26 % (17/38, proportion test: χ^2 = 0.24, p = 0.627) of the video recorded caches were stolen after 5 minutes of when the caches had been made. In none of the cases of cache theft was the thief an audience member during the original cache event (0/21, proportion test: χ^2 = 19.05, p < 0.001). Where caches were recovered, we found that the number of individuals present within a group had no effect on the time between caching and recovery (LRT, v_1^2 = 0.04 p = 0.840). The survival times of caches (8.28 ± 7.71 hours) were examined to determine if there was any effect of group size or cache placement patterns on this. The time from caching to theft was related to the number of individuals present (LRT, v_1^2 = 6.86, p = 0.009, Figure 2) but not to the rank of the cacher (LRT, v_1^2 = 4.40, p = 0.111). We found no relationship between cache survival time and either the distance caches were placed from the source (LRT, v_1^2 = 3.21, p = 0.073) or the NND of caches (LRT, v_1^2 = 3.21, p = 0.073). Results from our simulations on cache survival rates showed that with an increasing number of individuals, there was a linear decrease in the number of steps (analogous to time) required for a single food item to be uncovered (LRT, v_1^2 = -1154.3, p < 0.001, Figure 3a.). In addition, the proportion of simulations where a food item was uncovered was related to the number of individuals present within the group (LRT, v_1^2 = -9506.30, p < 0.001, Figure 3b.).

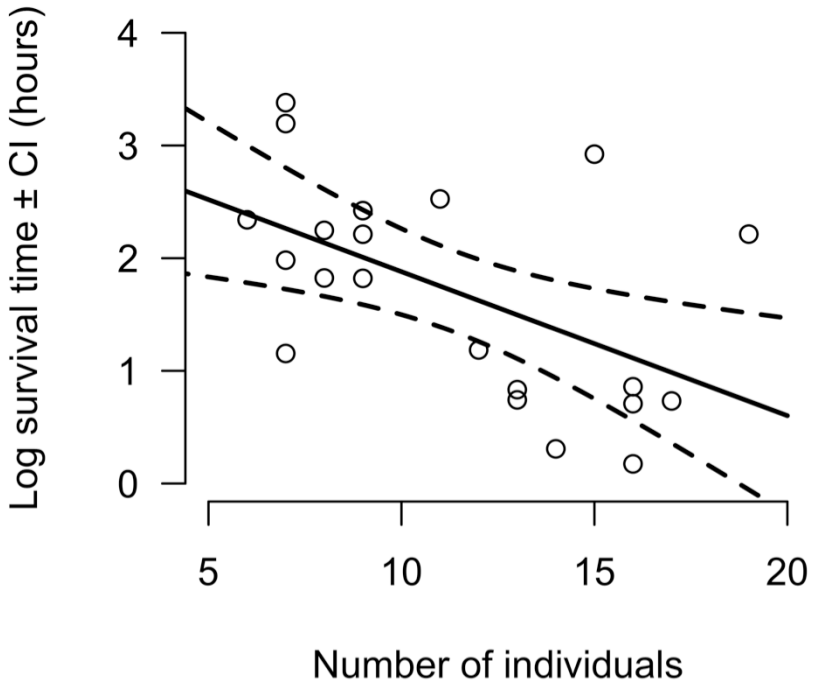

Figure 2: The relationship between the number of individuals present in the group and the amount of potential foraging time until the cache was stolen (n = 21) by a competitor. Confidence bands represented by dotted lines.

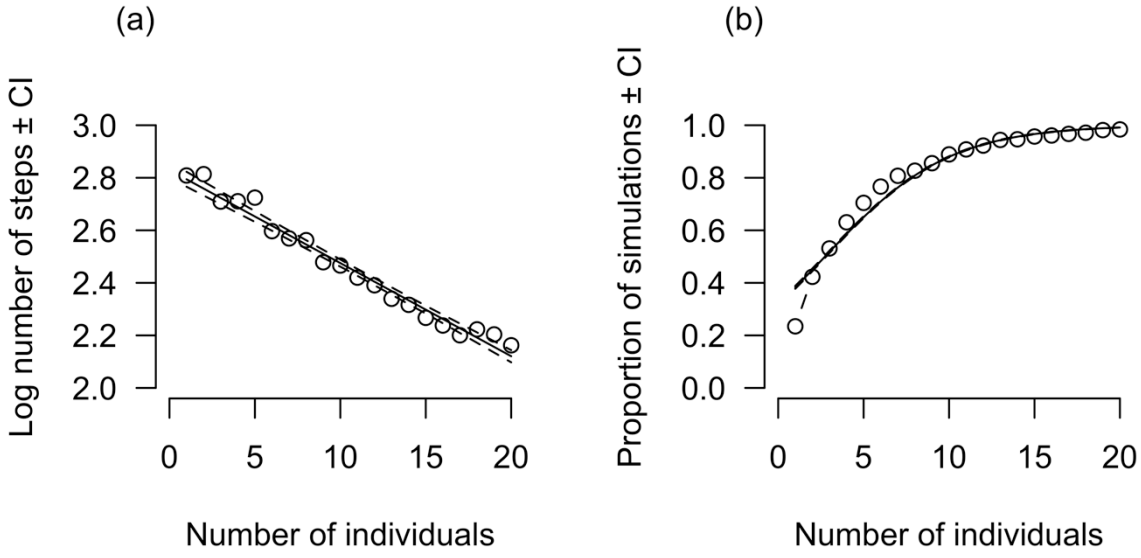

Figure 3: Results of the simulation model showing the number of individuals present within a group affecting the number of steps (a) until a cache was uncovered (analogous to time) and the proportion of simulations (b, $n_{\sum} = 2000$) where the food was found for each individual level.

Distance and NND constraints

Compared to theoretical predictions on the optimal distance and density caches to be placed (Stapanian & Smith 1978), we identified that the distance of caches from the burrow (LRT, v_1^2 = 1.65, p = 0.198, Figure 4a.) and the NND's (LRT, v_1^2 = 2.33, p = 0.127, Figure 4b.) were similar. The mean ± SD distance that caches were placed from the source was 29.78 ± 18.62 m (HE = 29.63 ± 13.75 m, IC = 33.24 ± 24.21 m, WK = 26.33 ± 14.90 m). Distances were normally distributed from the source to the furthest distance a cache was placed from the source (KS-test, D = 1.00, p = 0.276). There was no effect of the number of individuals in the group at the time of caching (LRT, v_1^2 = 1.78, p = 0.411) or the individuals' rank class (LRT, v_1^2 = 0.99, p = 0.320) on the distances that caches were placed from the source. To determine how caches were placed in relation to the general foraging patterns of individuals within their group home ranges, we used the location of animals during observational focals. The coordinates of caches were then compared to the convex hulls (95%) of the coordinates of individuals during the observations and in each of the three groups strong overlap was observed (% overlap of hulls, HE = 100.00 %, IC = 90.20 %, WK = 100.00 %). The mean ± SD distance animals were recorded from the centre of the burrow during these observations was 87.98 ± 88.61 m (HE = 71.46 ± 93.00 m, IC = 87.54 ± 82.83, WK = 89.89 ± 125.86 m), with a maximum distance of 978.51 m (HE = 978.51 m, IC = 566.61 m, WK = 694.42 m).

The mean ± SD NND was 9.51 ± 9.14 m (HE = 17.50 ± 8.58 m, IC = 13.38 ± 12.25 m, WK = 15.12 ± 13.19 m), with a mean area of 284.19 ± 262.65 m^2 between caches (HE = 308.36 ± 177.32 m^2, IC = 389.13 ± 430.98 m^2, WK = 107.60 ± 21.48 m^2). Similarly to the distances from the source, the NND's were not significantly different from a probabilistic normal distribution (KS-test, D = 1.00, p = 0.279). The number of individuals present (LRT, v_1^2 = 3.10, p = 0.078) or the rank of the cacher (LRT, v_1^2 = 0.96, p = 0.620) had no effect on the density at which caches were placed.

Proportion of food items cached to consumed

It was discovered that there was a strong propensity to consume rather than cache food when the number of individuals present was high (LRT, v_1^2 = 24.52, p < 0.001, Figure 5). There was no rank effect on the proportion of food being cached to being eaten (LRT, v_1^2 = 0.45, p = 0.978), nor was there an interaction with rank and the number of individuals present (LRT, v_1^2 = 0.45, p = 0.946).

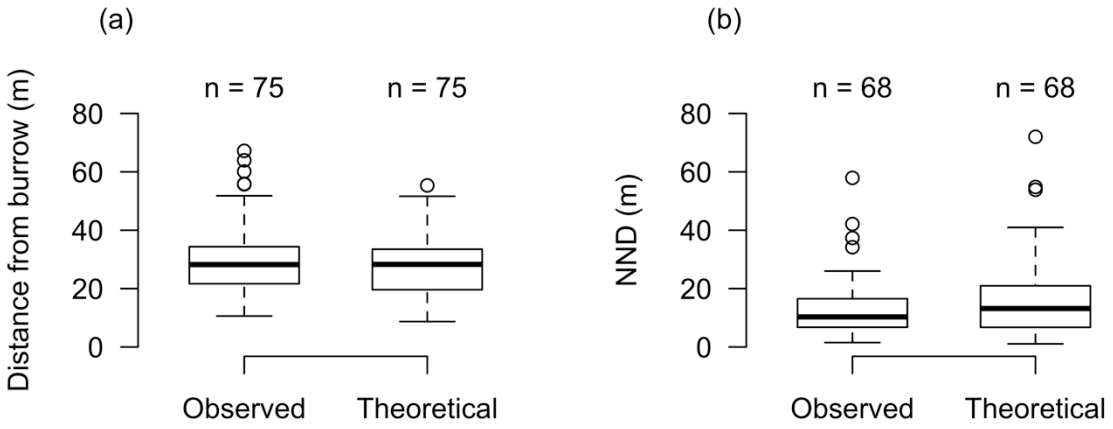

Figure 4: The observed and theoretical distances (median ± interquartile range) individuals should cache from the burrow centre (a) and the burrow source (b). The number of observations (N) are the same for both the observed and theoretical as the former was calculated from the latter.

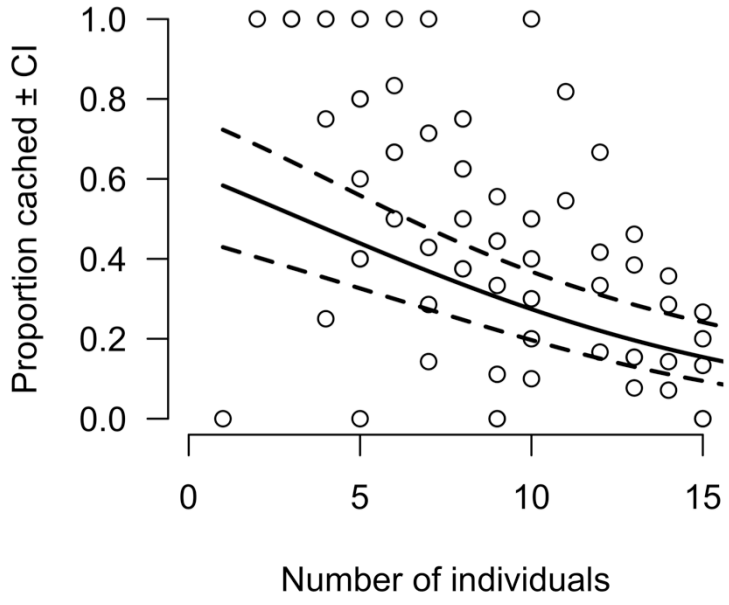

Figure 5: Proportion of food being cached to being eaten and the relationship to group size (n observational trials = 82).

Behaviour when caching

The absolute number of vigilance scans was neither related to the number of individuals present (LRT, v_1^2 = 0.13, p = 0.718) or the rank of the cacher (LRT, v_1^2 = 1.99, p = 0.370). Furthermore, there was no effect of the number of individuals present in a group on the rate of vigilance scans (LRT, v_1^2 = 0.55, p = 0.458) or the cachers rank (LRT, v_1^2 = 0.23, p = 0.891). In addition, where caches were re-cached, no relationship to the number of individuals present (LRT, v_1^2 = 1.84, p = 0.175) or the rank of the cacher (LRT, v_1^2 = 0.366, p = 0.833) was observed.

4. Discussion

Our study suggests that Cape ground squirrels were sensitive to their social environment and altered their decision to cache based on this. The lack of response in where caches were placed could be the result of squirrels caching at optimal distances and densities rather than altering placement in response to the risk of cache theft. In this species, as group size varies considerably across time periods, animals may benefit from showing flexible responses to differing numbers of competitors.

The number of individuals present in a group was directly related to the time it took for caches to be stolen. As no examples of audience members stealing caches at a later time were observed, we suggest this species does not exhibit "observational spatial" memory (Bednekoff & Russell 1996; Bugnyar & Kotrschal 2002). There was no effect of cache placement on the survivability and this along with the fact that audience members did not steal caches, suggests that delayed cache theft is random. In their study on black-capped chickadees, Stone & Baker (1989) suggest that competitors may uncover caches purely by chance, as they forage within the same home-range as the cachers. With group living central place foragers, the likelihood of random forager movement leading to cache discovery can be expected to increase with an increase in the number of foraging individuals (Fagan et al. 2007). Here we supported/confirmed this suggestion by using a random walk simulation to identify that increasing competitor number led to a reduction in the cache survival time and an increase in the likelihood an item would be uncovered.

We used the models described in Stapanian & Smith (1978) to determine the optimal distances from the source and NND of the caches made by the squirrels. Comparing the model to our results highlighted that individuals may be caching at optimal distance and density from the burrow. As the distance from the burrow

or the NND did not affect the survivability of a cached item, individuals may therefore be caching at distances and densities that maximise energetic gains rather than reducing cache loss. As there is a large difference between the edge of the home range and the mean distance of caches, individuals may be constrained to move beyond this to cache due to the risk of the costs outweighing the benefits of recovering an item. With the density of caches, the optimal distance may be too hyper-dispersed for a foraging competitor to uncover following food items. Rodents have been shown to engage in area-restricted searches once a food item has been uncovered, switching to a non-confined strategy when a successive food item is not uncovered within a given time period (Barton & Hovestadt 2013). In our example, due to the cache spacing, the likelihood of successive items being uncovered by a thief is low due to the large distance and therefore large search area between caches.

Rather than altering cache placement behaviour in response to conspecifics, we showed that individuals reduced the amount they cache. To explain this change in behaviour, we propose two competing hypotheses. The first suggestion is that individuals may perceive the causal relationship between group size and its impact on cache survival rates. Merriam's kangaroo rats (*Dipodomys merriami*) for example shift their strategy from scatter to larder hoarding in response to cache theft, but not in response to the mere presence of competitors (Preston & Jacobs 2005). This may suggest that this species perceives the effects of a changing social environment on cache survival. However, in our example, behavioural responses changed in relation to the number of competitors present during the caching episode. This would suggest that individuals not only perceive the relationship between competitor presence and cache loss, but also how this cache loss (or the survival time of caches) increases with competitor number. This is a potentially complex paradigm that may not be able to be learnt by individuals, and therefore we suggest a more parsimonious second hypothesis, that an increase in group size may cause behavioural changes not driven by these possible cognitive processes. For example nuthatches (*Sitta europaea*) respond to the presence of competitors by consuming more items than they cache (Carrascal & Moreno 1993). Behaviour such as this, instead of being driven by a perceived risk to a food item from conspecifics may arise through hormonal changes that cause shifts in behaviour. Circulating corticosterone levels have been shown to fluctuate with change in social group size (Pride 2005) and this hormone has also been implemented in causing a shift in caching behaviour (Saldanha et al. 2000). In their study (Saldanha et al. 2000) showed that an increase in corticosterone caused mountain chickadees (*Parus gambeli*) to recover more food efficiently and visit more cache sites. In our study, an increase in corticosterone may account for why we see a reduction in the amount of food cached

when group size increases. Pravosudov (2003) suggests that elevations in corticosterone may serve as an adaptation to unpredictable environments, by causing shifts in behaviour to maximise more efficient use of resources. To identify the effect of this hormone within this species, further experiments inhibiting/enhancing the levels of corticosterone will identify how changes in this hormone affects caching behaviour. The inability to recover faster when more competitors are present may be due to the re-location behaviours of this species, where there is a reliance on specific solar information in order for individuals to re-orientate back to a cache.

Unlike other studies on caching behaviour, we found no effect of social dominance on behaviour (Dally et al. 2005; Burns & Steer 2006; Toomey et al. 2007), possibly due to the scatter-hoarding behaviour of this species where aggressive defence of stores is not possible. Although individuals within differing levels of a social hierarchy may show variations in some behavioural responses (Lahti et al. 1998), a number of studies on rodents have shown that corticosterone is not influenced by rank (Chelini et al. 2011; Clarke & Faulkes 1998). Here, we suggest that potentially similar elevations in corticosterone across ranks due to increasing group size may cause similar behavioural responses in individuals. Where no behavioural responses in this study were observed, i.e. in cache placement behaviours, rank has been shown to have some or no effect on behaviour in other studies (Stone & Baker 1989; Lahti et al. 1998). In these studies, differences in rank effect may be due to the influence of immediate cache theft by higher ranked conspecifics (Dally et al. 2005), similar to what has been suggested in Cape ground squirrels previously (Samson & Manser 2015). However, in this study, we focused on delayed cache theft, where the rank class of the cacher did not affect the survivability of a food item. We therefore concentrated on social effects of caching that were not driven by audience member knowledge of the cache event.

Being sensitive to the social environment will be highly beneficial to an animal, where an increase in conspecific number will lead to increased competition. Selection may have acted on behaviour such as caching in this species to maximise resource acquisition in a high competition, low resource system. As caching food items allows for a build up of resources, this species may also profit from continuing to cache when the risk of cache loss from competitors is low. Such flexibility in the decision about when to cache will allow animals to secure resources in an environment where they are ephemeral and often limited in their occurrence.

5. Acknowledgements

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Caching in the presence of competitors: Are Cape ground squirrels (*Xerus inauris*) sensitive to audience attentiveness?

Jamie Samson & Marta B. Manser

Abstract

When social animals cache food close to their burrow the potential for an audience member to observe the event is significantly increased. As a consequence, in order to reduce theft it may be advantageous for animals to be sensitive to certain audience cues, such as whether they are attentive or not to the cache event. In this study, observations were made on three groups of Cape ground squirrels (*Xerus inauris*) in their natural habitat when they cached provisioned food items. When individuals cached within 10 m of conspecifics, we recorded the attentiveness (i.e. whether any audience members were orientated towards the cacher, had direct line of site and were not engaged in other activities) and identity of audience members. Overall, there was a preference to cache when audience members were inattentive rather than attentive. Additionally we found rank effects related to cache avoidance whereby high ranked individuals showed less avoidance to cache when audience members were attentive compared to medium and low ranked individuals. We suggest this audience sensitivity may have evolved in response to the difference in competitive ability amongst the ranks in how successful individuals are at winning foraging competitions. This study demonstrates that Cape ground squirrels have the ability to not only monitor the presence or absence of conspecifics but also discriminate individuals on their attentive state.

1. Introduction

Many animal species will cache food for a variety of different reasons (Vander Wall 1990), including to gain a disproportionate amount of an ephmeral resource (Dally et al. 2006), storing food for when natural stocks are reduced (Pravosudov & Grubb 1997) and protecting food resources from competitors (Balme et al. 2007). In scatter hoarding animals, where food is dispersed throughout a home range, stores are less prone to complete theft (Vander Wall 1990). However, in social scatter hoarders where conspecifics are always present, successfully storing food whilst reducing immediate loss is of fundamental importance (Heinrich & Pepper 1998). In solitary species, or those with overlapping territories, conspecific cache loss is also expected to occur but not at the frequency seen in social species (Vander Wall 1990). Previous research has shown that under these social pressures, animals may be sensitive to conspecifics (Leaver et al. 2007; Zhang et al. 2014a) and may show counteracting behaviours to ensure cache survival (e.g. Bugnyar & Kotrschal 2002; Steele et al. 2008; Hopewell & Leaver 2008).

Animals can be expected to cache food items only when the benefits gained from recovery outweigh the cost of caching (Andersson & Krebs 1978). Due to this energetic trade-off, social-species that cache may have to store food in less desirable locations, such as close to their home burrow and therefore, near conspecific competitors. However, caching can still be beneficial if the perceived risk of food loss is low (Lahti et al. 1998) or where animals show sensitivity to nearby conspecifics (Hopewell & Leaver 2008). If conspecifics are present, some species have been shown to engage in aversion behaviours that include reducing the frequency they cache (Lahti & Rytkonen 1996), concealing resources (Bugnyar & Kotrschal 2002), re-caching food (Emery et al. 2004) and behavioural deception (Steele et al. 2008). These behaviours, as suggested by Schmidt & Ostfeld (2008) function to reduce the amount of available information provided to a potential pilferer. However, it is still under debate as to whether these behaviours are due to social inhibition or some implicit understanding of the pilfering risk (van der Vaart et al. 2012; Thom & Clayton 2013). Western scrub jays (*Aphelocoma californica*) for example have been shown to use the shade when caching food to reduce the available visual information to potential pilferers (Dally et al. 2004; Dally et al. 2005). Such cache protection behaviours could have co-evolved with the ability of pilferers to steal caches. This may cause what has previously been referred to as an "arms race", which may have led to a "ratcheted-up" evolution of complex behaviours of both cacher's and thieves (Emery & Clayton 2004). However, in Western scrub jays where there are no distinct cacher and pilferer phenotypes: individuals can adopt both roles and transfer this knowledge across the two (Emery & Clayton 2001). In species with observational spatial memory, where conspecifics can remember the location of caches and pilfer at a later time (Bednekoff

& Balda 1996a; Bednekoff & Balda 1996b), cachers are expected to be highly sensitive to all animals close by due to delayed cache pilfering. In species which show no observational spatial memory, animals may benefit from showing flexible responses by only investing in cache avoidance or protection if, for example, audience members are higher ranked (Lahti et al. 1996; Pravosudov & Lucas 2000) or a known pilferer (Pravosudov 2008). For example, Lahti et al. (1996) described how removal of dominant willow tits (*Parus montanus*) from social groups caused animals to reduce the distance they cached from the centre of the home range. The response to specific cues from conspecifics, such as their knowledge about a cache event (Bugnyar & Heinrich 2005) has mainly been studied in corvids, however there is a lack of examples in mammals. For studies on mammals, research has mainly focused on the behavioural changes caused by the presence of conspecifics (e.g. Hopewell & Leaver 2008).

In this study, we provided Cape ground squirrels (*Xerus inauris*) with food items to cache and analysed whether cachers were sensitive to nearby conspecifics and their attentiveness, and whether they altered their caching behaviour accordingly. Cape ground squirrels provide a good system on which to study models of cache protection as this species is a social living central place forager (Waterman 1995) inhabiting a resource-restricted, open environment (Tshikae et al. 2013), which would suggest that they experience high levels of competition for resources. Groups typically consist of up to 19 individuals, with 1-3 reproductively active adult females and a number of subadults/pups of either sex (Waterman 1995; Waterman 1996; Hillegass et al. 2008). We predicted that squirrels would respond to the presence of audience members due to their sociality and scatter hoarding behaviour. When this species caches, a food item is initially uncovered and then individuals would move on average 17.02 ± 13.92 (mean ± SD) m away to bury the food, digging a hole of roughly 11.42 ± 3.20 cm in diameter and 4.23 ± 1.31 cm deep (unpublished data). Caching was more noticeable when high energy or "bonanza" resources were found, which often occurred after rain or strong winds (when food items were blown from trees; JS, personal observation). As this species has a structured (De Vries et al. 2006) but not linear social structure (unpublished data), we hypothesised that lower ranked cachers would show a higher sensitivity to conspecifics and their behaviour, as they would be less able to aggressively defend food compared to a high ranked individual. The sex of ground squirrels, in addition to rank was also considered, as males and females show divergent life-history strategies (Waterman 1995). Males often leave their resident group and prospect at neighbouring groups in a population to find receptive females to mate with (Waterman 1998). Therefore, female investment in caching may be higher than that of males, as females are more philopatric and can utilise stored resources more efficiently.

2. Materials and methods

Study site and study groups

The study was conducted in the natural habitat of the Cape ground squirrels at the Kuruman River Reserve, site of the Kalahari Meerkat Project in the Northern Cape, South Africa. Details of the habitat and climate are described in Brotherton et al. (2001) and Russell et al. (2002). At the study site, there were a number of groups that contained adults, subadults and pups of both sexes. We used three of these mixed sex groups that were habituated to close human observation (number of individuals mean ± SD; group 1 = 9 ± 2.00, group 2 = 13 ± 1.20, group 3 = 7 ± 0.63). As individuals dispersed or were recruited into these groups during the study period, group size was not consistent throughout. All individuals in these groups were sexed and uniquely marked using coloured hair dye (Garnier, L'Oreal, UK).

Observational data collection

Observations were collected from March - June 2013 during the afternoon, which coincided with the highest periods of caching (16:30 - 19:00 P.M.; JS, personal observation). Observations were undertaken on individuals (N = 14; group 1 = 3 males and 2 females, group 2 = 2 males and 3 females, group 3 = 3 males and 1 female) for 30 minutes, during which time animals were followed throughout. Observations were repeated six times for each individual across separate days; however, for 2 individuals a full set of repeats could not be achieved due to emigration of these individuals out of the groups. Therefore, over the course of the study, 69 observation sessions (group 1 = 22, group 2 = 28, group 3 = 19) were undertaken with 377 induced cache events recorded. To overcome any effects of behavioural changes due to variation in food quality (Preston and Jacobs 2009) that would have resulted from observing natural caching events, animals were provisioned with food (mean ± SD, 25 ± 0.25 mm size standardised peanuts in the shell). Food was given to individuals from the centre of their home range (hereafter; "source", which is analogous to the centre point of the sleeping burrow system) so that all distances moved were relative to these points. When animals cached, we recorded the distance from the source, distance to the nearest audience member, identity of audience members within 10 m and their rank and whether any audience members were attentive. Re-caching behaviour, where a hole was dug, the food item placed inside, and then removed and cached in another location was also recorded. In this study, only audience members who were within 10 m of the cacher were examined, as 95 % of targeted thefts (19/20 theft events) occurred when conspecifics were within a 10 m radius of the cacher. We only considered the highest-ranking audience member within 10 m of

the cacher as combining audience members' ranks will lead to a loss of statistical information (e.g. two medium ranked individuals will have the same average rank as high and low ranked individuals).

Animals were defined as being attentive to the cacher if their body was orientated towards the cacher with a direct line of site to the cache event (see Figure 1). Individuals that were facing the cacher but were engaged in other activities such as digging were noted as inattentive. A cache was defined as being "targeted stolen" if an audience member uncovered the cache within 60 seconds of the cacher placing the food item in a hole. This time frame was used as with targeted thefts, the thief usually stole the item immediately (17/19, 84.47 % of caches) after the cacher had moved away (JS, personal observation), after this the caches were normally not explored.

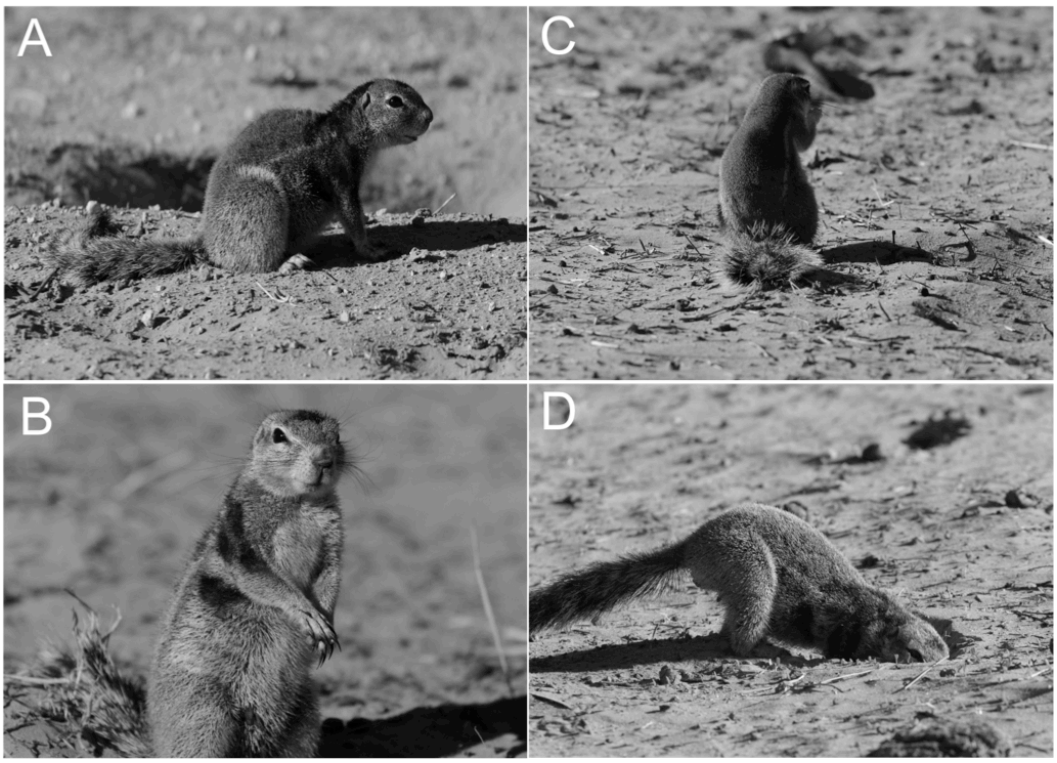

Figure 1: Categorisations of behaviours to define whether squirrels were attentive to a cache event or not. Pictures A and B, show squirrels that were defined as attentive, C and D inattentive. Attentive animals either had direct line of site to the cache (A) and/or their body was orientated to the cacher (B). If C and D behaviours were noted at the start of the cache event, but the individuals shifted to show A or B behaviours *during the cache event*, they were redefined as being attentive. With D, animals were only defined as inattentive if they remained with their head submerged in a foraging hole for the period of the cache event.

In addition to the observations described, we examined long-term data on foraging competitions to quantify if rank had an effect on the frequency at which animals would win competitions. These data were collected between March – June 2013 for all individuals within the three study groups. Foraging competitions were defined as when one individual approached another who was consuming or had uncovered a food item and an interaction occurred (e.g. aggressive fighting). For the purpose of this study, these data were split into two types, original owner won (where a forager retained the food item after a competitive interaction) and competitor won (where a competitor had succeeded in stealing food from a forager). The behaviour performed by the two animals was defined as either agonistic, where a fight, chase, or attack occurred or benign where either the forager blocked the approach of the competitor (i.e. turned its back), or the competitor simply approached the forager, but did not physically interact.

A Garmin GPS MAP62 handheld GPS device (Garmin LTD, 1996-2013) was used to record the coordinates of the caches and Garmin Basecamp (Garmin LTD, 1996-2013) was used to import and calculate the distance between the cache point and the source point (radial standard accuracy of ± 1.5 m). All observations were collected on a Palm TX Tungsten (Palm Inc, 2005) and transferred to Cybertracker data handling software (Cybertracker Conservation 2013). The distance to the nearest individual was estimated by eye, as audience members were constantly moving, and accurately taking GPS measurements was therefore not feasible.

Statistical analysis

All statistical analyses were performed in R, release GUI 2.1 (R foundation for statistical computing). Ranks of individuals were calculated using normalised David scores that were obtained from the analysis of agonistic association matrices ("steepness" package, De Vries et al. 2006). Individuals in groups were then ordered by rank and the groups split into three categories; high, medium and low rank classes. This was done because the hierarchies of the groups were not strongly linear (JS, personal observation) and therefore, the absolute rank value will not be as discrete as the rank class. Proportion tests (hereafter, "prop test") were used where analyses were performed comparing two proportions (null proportion = 0.5). Generalised linear mixed effects models (hereafter, GLMM; "lme4" package, Bates et al. 2014) were used to analyse the data, as these models allowed us to control for repeated measures and individual variation by assigning them as random factors. In all models, variance components were estimated using maximum likelihood ("ML") methods and additionally all random effects were kept in the models. As an unbalanced number of each rank class was observed during the study (high = 7, medium = 3, low = 4) all models were weighted to control for

this. For models where the sample sizes were low, post-hoc confidence intervals (hereafter CI, all at the 95 % level) were examined to determine if the models had sufficient explanatory power (Levine & Ensom 2001; Colegrave & Ruxton 2003). Where power was achieved with low samples sizes, CI intervals were included to show this. With the models concerning foraging competitions, statistical power was too low for a mixed modelling approach and therefore, weighted general linear models with a Poisson error structure (hereafter, GLM) were used. Where the overall effect of a factor was examined, we used likelihood ratio tests (here after LRT, ν) to compare models with the factors (or interaction of factors) included and excluded (Crawley 2007). As all model outputs only gave us the comparisons of the high ranked individuals with the other ranks, post-hoc multiple comparison tests with manually assigned contrasts were run to examine the differences between medium and low rank classes ("multcomp" package, Hothorn et al. 2008).

3. Results

The effect of audience attentiveness

Overall there was a strong preference for individuals to cache food over 10 m away from conspecifics (proportion = 265/377, prop test, $\chi_1^2 = 61.28$, $p < 0.001$) but there was no effect of the cacher's rank class on whether these caches were within or over 10 m from conspecifics ($v_1^2 = 1.06$, $p = 0.589$). Of the 112 caches placed within 10 m of conspecifics, 35 occurred when audience members were attentive and 77 when members were inattentive to the cache event (proportion = 35/112, prop test, $\chi_1^2 = 15.75$, $p < 0.001$, Figure 2a.).

The proportion of caches made in front of attentive as opposed to inattentive audience members was greater for cachers of the higher rank class (hereafter, mean ± SD; 9.71 ± 3.68) when compared to either cachers of the medium (7.00 ± 3.46, GLMM with binomial errors, z = -2.34, $p = 0.019$) or low rank classes (Figure 2b., 5.75 ± 3.86, GLMM, z = -2.49, $p = 0.013$). However, there was no difference in the proportion of caches made in front of attentive as opposed to inattentive audience members comparing the medium and low rank classes of cachers to each to other (GLMM with binomial errors, z = -0.05, $p = 0.963$).

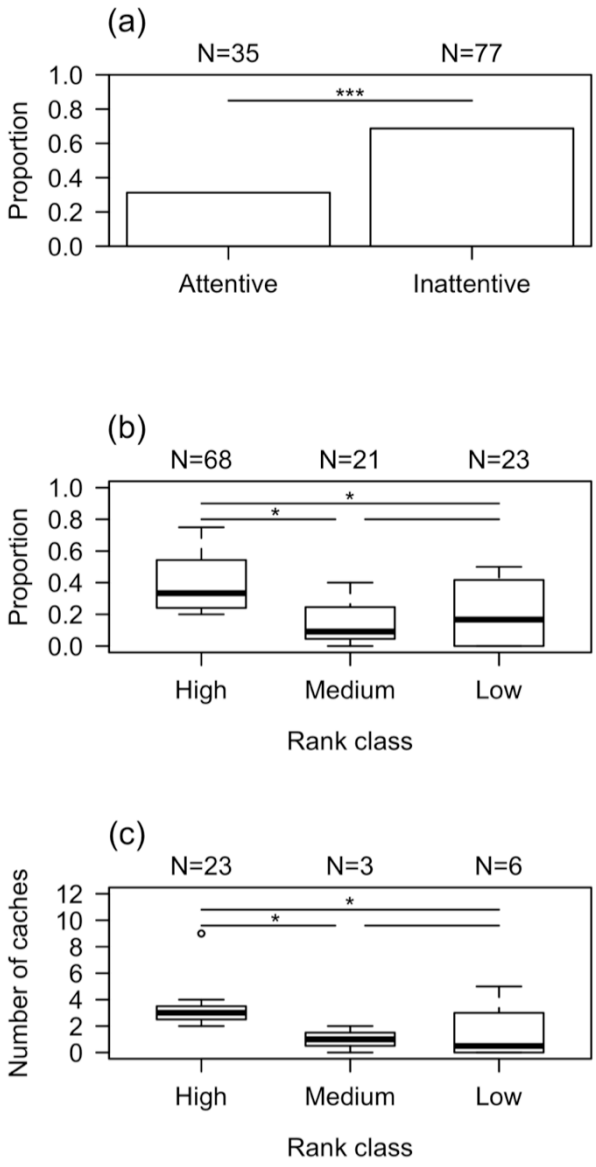

Figure 2. (a) The proportion of caches made when audience members were attentive or inattentive to the cache event. (b) Proportion of caches made when audience members were attentive as opposed to inattentive to the cache event for each of the three cachers' rank classes. (c) The number of caches made when audience members were attentive to the cache event for each cacher rank class (total number of subjects within each rank class for (b) and (c): high = 7, medium = 3, low = 4). The 'N' above the boxes refer to the total number of events recorded for all individuals. Hereafter, asterisks denote the significance level of the p-values; * < 0.05, ** < 0.01, *** < 0.001, where an absence of an asterisk indicates no significant difference was found (i.e. $p > 0.05$).

Where individuals were attentive to the cache event (Figure 2c.), the same results were obtained, with caching individuals in the high rank class (3.71 ± 2.43, CI[0.44,1.89]) making a greater number of

caches compared to cachers of medium (1.00 ± 1.00, GLMM with Poisson errors, z = -2.09, p = 0.037, CI[-3.08, 0.06]) and low rank classes (1.5 ± 2.38, GLMM with Poisson errors, z = -2.81, p = 0.026, CI[-3.08,-0.27]). Medium and low ranked individuals cached an equal number of items when audience members were attentive (GLMM with Poisson errors, z = -0.01, p = 0.989). Although there was no effect of rank (GLMM with binominal errors, v_1^2 = 2.71. p = 0.608), overall individuals were more likely to cache a food item as opposed to re-caching it when individuals were inattentive to the cache event compared to being attentive (GLMM with binominal errors, v_1^2= 14.58. p < 0.001). Where individuals did re-cache, a higher proportion of caches were made when individuals were inattentive to the re-cache event (proportion = 76/103, prop test, χ_1^2 = 22.37, p < 0.001).

Although there was no effect of a cacher's sex (GLMM with binomial errors, v_1^2 = -0.13, p = 0.900), there was a significant interaction between a cacher's sex and rank class for the proportion of caches placed in front of attentive as opposed to inattentive audience members (GLMM with binominal errors, v_1^2 = 7.29, p = 0.026). For females, the proportion of caches placed in front of attentive as opposed to inattentive audiences members declined across rank classes from high to low, whereas the opposite pattern was observed for males. Comparing the cachers' sexes within each rank class showed that there were no differences in the caching proportion within high (GLMM with binomial errors, z = 1.19, p = 0.236) or medium (GLMM with binomial errors, z = 1.32, p = 0.187) rank classes, but there was within the low rank class (GLMM with binomial errors, z = 2.04, p = 0.041).

Cache theft

We examined the immediate cache survival (within 5 minutes of the cache being made) to determine if this was affected by the attentive state of audiences members. Within this period, a greater proportion of caches were stolen as opposed to survived (overall proportion of stolen caches = 11/101) when audience members were attentive (7/28 events where a cache was stolen and an audience member was attentive) as opposed to inattentive (4/73 events where a cache was stolen and an audience member was inattentive, v_1^2 = 5.91, p = 0.015). There was no overall effect of rank class on whether caches were immediately stolen (GLMM with binominal errors, v_1^2 = 0.02, p = 0.992).

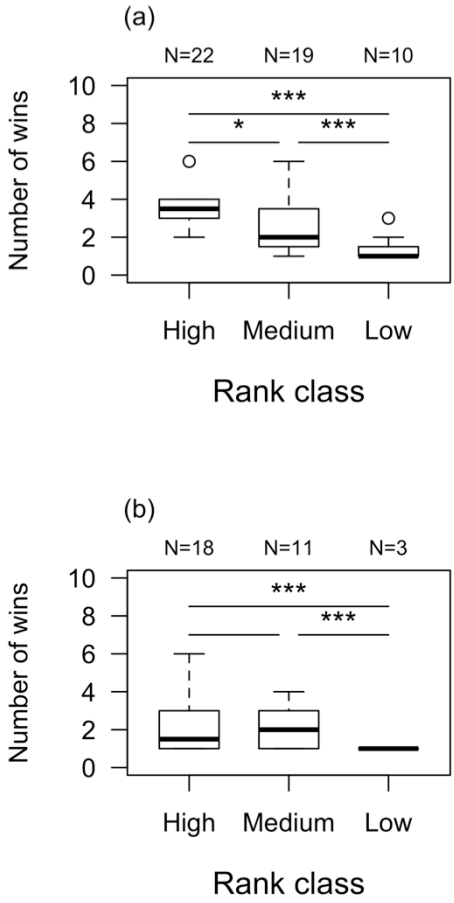

Figure 3: The number of foraging competitions won by individuals in each rank class when (a) the winner was the original owner or, (b) the winner was the competitor. For both of the figures, the total number of subjects within each rank class was, high = 10, medium = 10, low = 9. The 'N' above the boxes refer to the total number of events recorded for all individuals.

Foraging competitions

If the original owner of the item won the foraging competition (Fig. 3a, i.e. retained the food item, N = 51 interactions), high rank class (4.00 ± 3.00, CI_{high}[1.12, 1.47]) individuals showed greater success at retaining the item, compared to medium (3.00 ± 2.45, GLM with Poisson errors, z = -2.45, df = 15, p = 0.014, CI_{medium}[-0.54, -0.06]) and low ranked individuals (1.40 ± 0.88, GLM with Poisson errors, z = -6.38, df = 15, p < 0.001, CI_{low}[-1.24, -0.66]). Medium ranked individuals were also more successful than low ranked individuals (GLM with Poisson errors, z = -4.347, df = 15, p <0.001). Where competitors were winners (Fig. 3b), i.e. individuals stole an item from a forager (N = 32 interactions), we saw a similar pattern, with low (1.00 ± 0.00) ranked individuals winning less competitions than either high (2.25 ± 1.75, GLM with Poisson errors, z = -3.4, df = 15, p <0.001, CI_{high}[0.62, 0.99], CI_{low}[-1.31, -0.37]) or medium ranked individuals (2.20 ± 1.30, GLM with Poisson errors, z = 3.20, df = 15, p = 0.001, CI_{medium}[-0.32, 0.26]). High ranked individuals

were equally successful at winning these contests as medium ranked (GLM with Poisson errors, z = -1.15, df = 15, p = 0.880). During foraging competitions, agonistic interactions were recorded in 43% (N = 34) of the cases and benign in 57% (proportion = 34/83; prop test, $\chi_1^2 = 2.061, p = 0.151$).

4. Discussion

In our study we investigated how during cache events, wild Cape ground squirrels responded to the attentiveness of audience members, and found this response was more pronounced in lower and medium ranked individuals. Audience attentiveness was also shown to affect whether a cache was stolen, which may help explain why individuals are sensitive to this behaviour. In addition, the competitive abilities of individuals were examined during foraging competitions, which highlighted that lower rank classes were less successful than higher rank classes at winning these.

As we saw strong rank class effects on whether a cache was made in the presence of attentive or inattentive audience members, individuals may have some knowledge of their rank within a group. A few studies have illustrated how individuals alter their caching behaviour in response to more dominant individuals (Clarke & Kramer 1994; Lahti et al. 1996; Lahti et al. 1998; Dally et al. 2005). For example, in Eastern chipmunks (*Tamias striatus*) it has been shown that dominant individuals prefer to larder hoard, as they are better than subordinates at defending food stores (Clarke & Kramer 1994). In the Cape ground squirrels higher ranked individuals were more likely to retain food items during foraging competitions, which may explain the reduced response to audience attentiveness in this rank class, and also the reason we find higher sensitivity in both medium and lower ranked classes. In both female chimpanzees (*Pan troglodytes*, Wittig & Boesch 2003) and capuchin monkeys (*Cebus paella*, di Bitetti & Jansen 2001) for example, dominant individuals are able to monopolise and retain food items over subordinate group members. These results indicate one of the ways in which selection pressure may have acted on this sensitivity to attentiveness, and why we see differences amongst rank classes.

Where audience members are attentive to a cache event, it pays for individuals to alter their behaviour to reduce the risk of theft and/or a competitive interaction. One of the ways a number of different species have been shown to do this is through re-caching, when individuals move a food item from one site to another (Emery et al 2004; Zhang et al. 2014b). In this study, individuals made more re-caches when audience members were attentive to the original cache event. In addition, where individuals did re-cache,

they did so where individuals were inattentive to the re-cache event. This re-caching behaviour may be a by-product of social inhibition (Clayton et al. 2007), caused by the attentiveness of audience members, although to confirm this requires further testing.

Being knowledgeable to what competitors can or may see, can infer a selective advantage to cachers, over responding merely to the presence of competitors (Preston & Jacobs 2001; Steele et al. 2008; Hopewell & Leaver 2008). This means that they do not engage in cache protection strategies (Dally et al. 2006) simply based on whether conspecifics are present or not, but adjust their behaviour in relation to that of the behaviour of audience members (Bugnyar & Heinrich 2005). In some corvid species, there is the suggestion that the use of avoidance tactics under certain conditions may infer these behaviours are under some 'sociocognitive' control (Emery & Clayton 2001) and additionally individuals may also use their own experience of stealing other individual's cachers in their own cache protection. However, responding to the attentiveness of individuals does not necessarily require complex cognitive processing by the cacher. In this study, we suggest that animals may learn to avoid caching in the presence of certain attentive audience members through repeated foraging competitions that often result in agonistic interactions such as sustained fights. Through associative learning processes, individuals may acquire information regarding how the behaviour of audience members may lead to costs, in terms of losing a food item or the risk of a fight (Miklósi et al. 1995). As lower ranked individuals are more likely to lose foraging competitions, these individuals may become sensitive to audience attentiveness through negative associations with a loss of a resource (Yi-Ting & Hsu 2011).

We found an interaction between sex and rank class, which suggests that the effect of rank class differs between the sexes in terms of caching behaviours (Vander Wall 1990; Brodin & Urhan 2015). Female ground squirrels are more philopatric than males (Waterman 1995), with males showing year round prospecting behaviour at neighbouring groups (Waterman 1998). Females could therefore rely more heavily on cached food that may have caused females to evolve a higher sensitivity to the surrounding audience (Brodin & Urhan 2015). Jenkins (2011), examined sex differences in two species of kangaroo rat and suggested divergent cache behaviour may be a consequence of different life history strategies. In addition, sex differences may result from a females need to acquire resources during breeding, where they may invest more in caching to overcome reproductive costs, in particular when food is scarce (Steer & Burns 2008). As female Cape ground squirrels are all year round breeders and display low reproductive skew (Waterman 1995, Waterman 1996), all adult females have the potential to breed. Therefore, variation in competitive ability across ranks may be linked to why we see a stronger avoidance to cache in the presence of attentive

audiences members for low ranked females. Higher ranked males may show this heightened sensitivity to attentive audience members as a strategy to reduce conflict, as in this study these adults were immigrants in to their groups (Smale et al. 1993).

As Cape ground squirrel social structures are temporally dynamic (J.S. unpublished data), future studies could be used to determine if and when animals change rank class, this is reflected in their caching behaviour. We would predict that as an animal moves higher up the dominance hierarchy their caching behaviour shows a delayed transition to reflect this change in rank. Additionally, if animals were deposed from a high rank class, we would predict that they might increase their sensitivity to audience attentiveness. Such results will allow us to determine the degree to which these rank-specific effects (and sensitivity to) are flexible and how long it takes for an animal to show responses representative of their rank.

Although a number of studies on food storing mammals have shown how individuals can respond to the presence/absence of audience members (Preston & Jacobs 2001; Steele et al. 2008; Hopewell & Leaver 2008), here we show how a mammal can respond to the attentive state of audience members. Such studies have received a great deal of attention in birds (Dally et al. 2006), but there has been a lack of studies on mammals. However, in contrast to various studies on corvids (Emery & Clayton 2004), we argue that in this species, the responses shown may have evolved through associative learning mechanisms and not as a by-product of advanced cognitive capabilities.

5. Acknowledgements

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Are Cape ground squirrels (*Xerus inauris*) sensitive to variations in the payoffs from their caches?

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Abstract

For food caching to be adaptive, the benefits of recovery must outweigh the costs of storing an item. One of the costs to cachers is the risk of theft, and therefore, it is predicted that individuals may be sensitive to this theft and show various behavioural strategies to minimise it. In this study, we gave wild Cape ground squirrels (*Xerus inauris*) a choice between two different coloured items of the same food type: one item with a specific colour that was always artificially removed when cached and the other item with a different colour that was not removed when cached. During the choice presentations, subjects reduced the amount they consumed and cached of the food items with the colour that was experimentally removed when cached, despite the two items only differing in caching pay-off. This avoidance to choose the food with the colour that was removed occurred over time, which suggests that subjects were using information about the item's pay-off during cache recovery and this then impacted on successive decisions. This study highlights how the sensitivity to a food item's pay-off can affect an individual's choice towards items that offer the greater overall reward.

1. Introduction

Animals constantly face decisions that could have repercussions on their future fitness (McFarland 1977; Stevens 2008). One of the traditionally accepted assumptions of decision-making models is that evolutionary pressure has selected animals to behave 'optimally' (McFarland 1977; Kalenscher & van Wingerden 2011). An area that has been extensively studied is the optimal decisions animals make when foraging whereby animals are expected to maximise their rate of energy gain (Charnov 1976; Cowie 1977). In behaving optimally, individuals must balance the units of energy gain, such as intake rate against the cost of adopting that foraging strategy (Pyke et al. 1977; Pyke 1984). Costs can refer to a variety of factors such as predation risk (reviewed in Lima & Dill 1990), energetic pay-off (Richardson & Verbeek 1986) or competition (Lawlor & Maynard Smith 1976; Pimm & Rosenzweig 1981). The ability of an animal to forage optimally will therefore have a significant impact on their fitness (reviewed in, Pyke 1984).

One foraging strategy is to cache food upon discovery, storing it for later consumption (Vander Wall 1990) over both short and long periods (Cowie et al. 1981). Food caching in animals is only expected to occur where the pay-off to the cacher, in terms of recovering an item is greater than the investment in caching (Andersson & Krebs 1978; Stapanian & Smith 1984). Animals should therefore be sensitive to the pay-offs from their cached food items, altering their behaviour in relation to the net gains (Luo et al. 2014). Where cache loss occurs, species appear to engage in cache protection strategies to minimise this theft (Dally et al. 2006). Examples include being sensitive to the knowledge or attentiveness of audience members to a cache event (Bugnyar & Heinrich 2005; Samson & Manser 2015) or displaying deceptive strategies (Bugnyar & Kotrschal 2002; Steele et al. 2008). The type of cache protection strategy employed by a species is linked to a number of factors such as cognitive capabilities (e.g. scrub jays, *Aphelocoma californica*, Clayton et al. 2007), sociality (e.g. Ord's kangaroo rat, *Dipodomys ordii*, White & Geluso 2012) and cache type exhibited by that species (i.e. larder vs. scatter hoarding, Preston & Jacobs 2005; Zhang et al. 2011). One such cache protection strategy that is suggested to require advanced cognitive capabilities is exclusion performance.

Exclusion performance is defined as 'selecting the correct alternative by logically excluding other potential alternatives' (Call 2006; Mikolasch et al. 2012). One of the underlying assumptions of this exclusion performance ability is that animals must be spontaneous in their success (Call 2004), as gradual changes in decisions may suggest this behaviour is instead controlled by learning mechanisms (Schloegl

et al. 2009). The ability to display exclusion in corvids has been linked to caching behaviour (Schloegl et al. 2009) where related non-caching species, such as jackdaws (*Corvus glandarius*), show an inability to successfully complete the same tasks (Schloegl 2011). In caching corvid species, exclusion may have evolved due to the cognitive demands associated with caching, whereby this exclusion behaviour allows individuals to keep track of the contents of their caches (Schloegl 2011; Mikolasch et al. 2012). However, this relationship has recently come under some scrutiny, where a study on another caching species, the Eurasian jay (*Garrulus glandarius*) did not find evidence of exclusion behaviour (Shaw et al. 2013). The inability of a species such as scrub jays to show spontaneous responses in cache tasks may be due to the fact that critical learning may occur at the time of recovery (Clayton et al. 2005). Therefore, animals may accumulate information about the profitability of a food item/site at recovery and use this information in subsequent cache decisions (Clayton et al. 2005).

We investigated whether manipulating the pay-offs of food items, within the context of food caching, would cause the Cape ground squirrel (*Xerus inauris*) to alter their caching behaviour. This species is an ideal study system to test this question due to their high degree of sociality (Waterman 1995), the harsh environment they live in (Tshikae et al. 2013) and their scatter-hoarding tendencies (Samson & Manser 2015). Together, these factors suggest that this species could be under intense competition for a limited amount of resources, which may select for sensitivity to conditions that lead to loss of these resources to competitors. Other rodent studies on food caching have highlighted a number of species to be sensitive to complete cache pilferage (where all items were removed, Huang et al. 2011; Luo et al. 2014), whereas here we tested whether subjects were sensitive to unequal cache pilferage rates between two items. We tested whether subjects would shift their behaviour in relation to the pay-off of the food item in order to choose items with the highest pay-off. Secondly, we predicted that this choice would be context specific, with subjects only showing variation in choice with respect to the food they cached and not consumed when food was provided. Huang et al. (2011) and Luo et al. (2014) suggested that the response of a rodent species to complete cache pilferage showed some degree of behavioural plasticity, but not at the level observed in some caching corvid species (Schloegl 2011). Therefore, thirdly, we predicted that our subjects would develop choice preference over presentation sessions, as individuals associatively learn the dichotomous cache pay-off of each item. Finally, we predicted that the variation in recovery potential of each of the two food colour types would cause individuals to show divergences in the spatial arrangements of caches in response to the perceived cache theft. It was shown in Merriam's kangaroo rats (*Dipodomys merriami*) that they switched

from scatter to larder hoarding when cache theft was high, as concentrated stores were easier to defend (Preston & Jacobs 2001). However, Cape ground squirrels are highly social and have structured hierarchies (Samson & Manser 2015), meaning aggressive defence of single stores is unfeasible, due to the intensity of competition and the variation in competitive ability between individuals. Rather than larder hoarding the stolen food item type, we hypothesised that individuals would cache further away from their groups' central burrow and at lower densities to minimise cache loss (Clarkson et al. 1986).

2. Materials and Methods

Ethical Note

This work was undertaken in accordance with the guidelines outlined by the University of Pretoria, Animal Ethics Committee permit, no. ECO14-14.

Study Site and Species

This study was conducted at the Kuruman River Reserve, a research station located in the Kalahari Desert in South Africa (26°58′S, 21°49′E, Brotherton et al. 2001). At this site, Cape ground squirrels naturally occurred and a number of groups were habituated to close human observation (< 1 m) and all individuals within these groups had been given a unique dye mark (Samson & Manser 2015). This species is a highly social central place foraging sciurid that inhabits arid regions of southern Africa (Waterman 1995; Hillegass et al. 2008). Cape ground squirrels 'scatter-hoard' food around a central burrow and peaks in caching are observed after the heaviest periods of rainfall (J. Samson, unpubl. data). This species is also a short-term hoarder (Vander Wall 1990), as food caches are typically recovered food within 24 h of being made (Samson & Manser 2015). We tested 10 wild adult squirrels for this study (females = 6, males = 4) from six different social groups. Adult individuals were those over 12 mo of age, and due to large testis size, sex was easily determined (Waterman 1998). As the marked population has been maintained since May 2012, the age classes of all individuals used in this study were known (4 of 10 individuals where exact age was known, 6 of 10 individuals were present since the start of the project, being all older than 3 yr).

Experimental Design

In this study, we tested two experimental groups, 'coloured removed' and 'non-coloured removed', which corresponded to the food type that was removed after being cached by the animal during the manipulation

phase (the other food item was not manipulated, Table 1). During the control condition, the observer manipulated no food items, but the coloured and non-coloured foods were presented. Each subject was assigned one of these two experimental groups using a randomised binary number generator, in a balanced design (n = 5 for each condition, Table 1). The food was standardised 2.5-cm-long monkey nuts (peanuts in the shell) that were either coloured or non-coloured. As no studies have been conducted on the visual abilities of this species, we assumed they are mono/dichromatic, as has been previously shown for other species of sciurids' (Jacobs 1978). Therefore, in this study, we used blue dyed (the shell coloured with blue food dye) and uncoloured nuts, which would appear distinct from each other.

Procedure

Subjects were presented with two identically sized food items, one coloured and one non-coloured nut, in a shallow cup attached to the end of a 1.5-m pole. Before the cup was placed on the ground, it was covered and shaken for 5 s to randomise the position of the two nuts. The cup was then placed on the ground, and the subject was allowed to approach the cup and choose an item, and once an item was chosen, the cup was lifted to stop the other item being taken. To reduce side bias, if the subject approached at an angle to the cup, it was lifted and placed again until the subject approached straight on (Fig. 1). This procedure was repeated up to four times for each subject during each presentation session (Table 1). When a food item was chosen, the choice (coloured or non-coloured) and fate (cached or eaten) were noted down. When subjects cached food items, a GPS point of the cache was taken. In addition, any caches (during the manipulation condition) of the removed item colour category were marked with non-descript cocktail sticks. As squirrels were never observed returning to caches during the period presentations were undertaken, individuals would therefore not associate the sticks with their caches. After the squirrels went below in to the sleeping burrow for the night, the cache sites for the removed items category were revisited and the food (and marker sticks) removed. When food was removed, the observer wore latex gloves to limit olfactory contamination of the cache site. All presentation sessions in this experiment were conducted in the afternoon, 1.5 h before individuals went below in to their burrows for the night to control for the motivational state of individuals. In addition, as subjects slept in the same burrow each night and returned to the burrow when they had ceased foraging, conducting presentations at this time allowed us to more easily locate the subjects. Sessions for each subject were terminated once four trials were completed or 30 min had passed since the start of the session. Trials were repeated within presentation sessions to ascertain average choice, rather than using a

single trial. However, as caches were only manipulated after the presentation sessions had ceased, within these sessions no learning effects with respects to the item colour type's pay-off would occur.

Table 1: Experimental design used in this study. To control for condition level effects, we had a balanced number of subjects in both the non-coloured removed (n = 5) and the coloured removed (n = 5) levels. Within each presentation session, four replicate trials were attempted, but in three sessions a full set of repeats was not obtained within the 30 minute time limit.

	Control *No caches removed*		**Manipulation** *Caches of coloured or non-coloured food items removed based on assigned condition*							
Presentation session	1	2	3	4	5	6	7	8	9	10
Coloured food removed	3	4	4	4	4	4	4	4	4	4
	4	4	3	4	4	4	4	4	4	4
	4	4	4	4	4	4	4	4	4	4
	4	4	4	4	4	4	4	4	4	4
	4	4	4	4	4	4	4	4	4	4
Non-coloured food removed	4	4	4	4	4	4	4	4	4	3
	4	4	4	4	4	4	4	4	4	4
	4	4	4	4	4	4	4	4	4	4
	4	4	4	4	4	4	4	4	4	4
	4	4	4	4	4	4	4	4	4	4
Number of trials conducted	39	40	39	40	40	40	40	40	40	39
									Total	**397**

Cache fate and placement analysis

To determine whether caches were stolen by conspecifics or recovered by the cacher, we set up remote cameras near the site for 5 d and recorded 15-s videos whenever the infrared component was triggered (5210A series, LTL-Acorn Outdoors). As we could identify the individuals who removed caches, we could

quantify an estimate for the proportion of caches recovered by the cacher or stolen by a conspecific. The distance caches were placed from the source (i.e. the centre of the burrow and where the choice task was presented) was determined by convertig all coordinates from Cartesian to UTM and then calculating the Euclidean distance between the source and cache coordinates. Cache density was resolved by extracting within session nearest neighbour distances (NND) of caches for each subject animal. The NND was calculated using an in built function in the 'spatstat' package in R (Baddeley & Turner 2005).

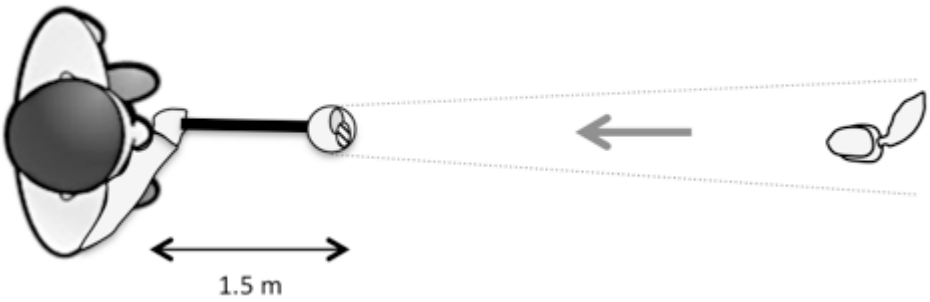

Figure 1: How the choice task was presented to individuals during the trials. The pot was placed on the ground and the squirrel was allowed to approach, and if the subject did not approach straight on (as indicated by the grey arrow), the pot was lifted and the trial reset. During the presentations, the observer did not make eye contact with the squirrel and had their free hand down by their side.

Statistical analysis

All statistical analyses were performed in R; release GUI, version 3.2.0 (R Core Team 2015). Generalised linear models (hereafter, GLM) with a Poisson error structure were used to analyse the number of food items chosen during the control condition. These models were conducted to determine whether there was any pre-existing preference for the caching or consuming the coloured or not coloured food items. Generalised linear mixed models (Bates et al. 2015) with a binomial error structure were used to analyse the choice data, as the outcome variable was binary (removed or non-removed items chosen). Condition (control or manipulation) and presentation session number (Table 1) were assigned as explanatory variables in the overall and presentation models, respectively. Experimental group (coloured or non-coloured food item removed), group and individual were assigned as random factors; in addition, trial number was included to control for repeated

measures. As the number of individuals present in a group has been shown to negatively impact on the frequency at which food is cached as supposed to consumed (JS unpublished), we also included number of individuals as a random effect in the models. The number of individuals present refers to the total number of individuals counted by the observer at the group during that presentation session (all individuals were included in this count and not just those visible to the study subject). Linear mixed effect models were used to analyse the cache placement data, incorporating the same random effects as the first models. Significance of the explanatory variable for the mixed models was determined using likelihood ratio tests (hereafter, LRT, Crawley 2007), where models with the explanatory variables were compared to models with the explanatory variable removed. In all models, variance components were estimated using maximum likelihood methods, and additionally, all random effects were kept in the models. All p-values are two-tailed, and the significance level was set at 0.05.

2. Results

Across a total of 397 presentations, 230 food items were cached and 167 immediately consumed (number of items cached: total number of presentations, prop test; $\chi_1^2 = 9.68$, p = 0.002). Within the control condition, we found no pre-existing preference for caching either the coloured or non-coloured food items (GLM, $z = 0.88$, df = 19, p = 0.378) or a preference to consume either coloured food item (GLM, $z = -1.21$, df = 17, p = 0.227, Fig. 2). Subjects chose a higher proportion of items of the non-removed food colour type compared to the artificially removed food colour type comparing across conditions (proportion of non-removed/removed, manipulation: 177/141, control: 34/45, LRT, $v_1^2 = 4.17$, p = 0.041, Fig. 3a). No difference was observed in the proportion of food cached or consumed across conditions comparing both removed and non-removed items (LRT, $v_1^2 = 1.51$, p = 0.219). Where animals chose the removed item colour type, no difference was observed in the proportion of food cached or consumed across conditions (LRT, $v_1^2 = 0.60$, p = 0.438). Over manipulated presentation sessions, subjects chose a higher proportion of non-removed food colour type compared to the removed (LRT, $v_1^2 = 7.54$, p = 0.006, Fig. 3b). No difference was observed in the proportion of food cached or consumed across manipulated presentation sessions comparing both removed and non-removed items (LRT, $v_1^2 = 0.01$, p = 0.920). In these manipulated presentation sessions, where animals chose removed items, no difference was observed between the number of items cached or consumed (LRT, $v_1^2 = 0.51$, p = 0.474).

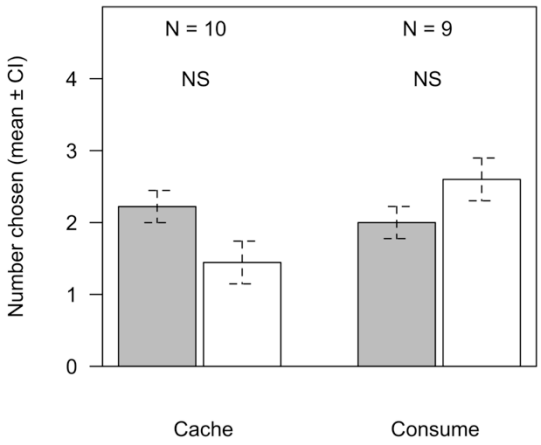

Figure 2: The number of coloured (grey) and non-coloured (white) food items cached and consumed in the control part of this study (the dashed lines represent the confidence intervals (CI) calculated from the model predictions). This figure only shows the control data so that we can highlight how there were no pre-existing preferences to consume or cache either colour. The N refers to the number of subjects within each category (cache or consume). Only nine subjects appear in the consumed model, as one test subject cached all food presented. NS: $p \geq 0.05$; *:$p < 0.05$; **:$p < 0.01$; ***:$p < 0.001$.

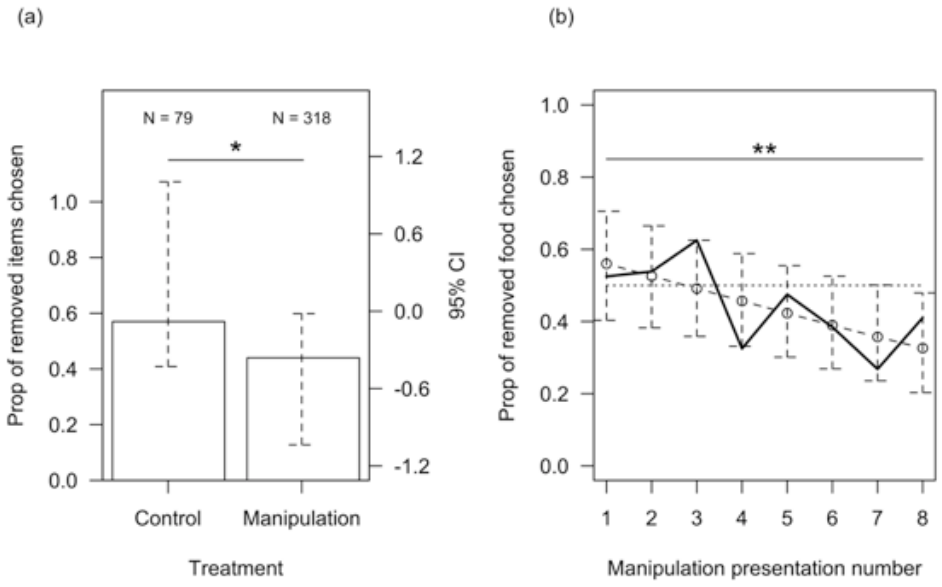

Figure 3: (a) The proportion of items chosen of the removed food type changed between the control and manipulated presentations of the study (white bars with the 95% confidence intervals (CI) extracted from the model, dashed lines). The N above the plot refers to the total number of choice trials conducted in each condition. (b) The change in the proportion of items chosen of the removed food type over the 8 manipulated presentation sessions (solid black line). The dashed lines and open circles show the model predictions (± 95% CI) for each manipulated presentation session. NS: $p \geq 0.05$; *:$p < 0.05$; **:$p < 0.01$; ***:$p < 0.001$.

Comparing control to manipulated presentation sessions, items of both food colour types were cached at similar distances from the centre of their home range (Table 2). Over the manipulated presentation sessions, there was no change in how far food items of either colour category, the removed or non-removed items, were placed from the source (Table 2). We found a similar pattern with cache density, with no difference between the control and the manipulated presentation sessions in how caches were dispersed for either food colour type or whether density changed over trials (Table 2).

Table 2: Effect of item choice (removed or non-removed food type) on the distance and density at which caches were placed.

Model	Estimate	SE	v_1^2	p
Distance from source				
Across treatments	0.11	0.36	0.10	0.951
Manipulated presentation sessions	0.05	0.07	1.78	0.411
NND				
Across treatments	0.05	0.18	-0.74	0.604
Manipulated presentation sessions	0.05	0.39	1.73	0.421

When quantifying the amount of caches recovered by the cachers or stolen by conspecifics, we found 27 of 47 caches (57.4 %) were stolen and the rest were recovered by the cacher (proportion test; χ_1^2 = 0.77, p = 0.382). Therefore, in this experiment, the two items have a predicted 43.6 % (non-removed) to 0 % (removed) return rate, accounting for this natural loss in food (a payoff ratio of 0.44:0).

4. Discussion

This study demonstrates how Cape ground squirrels can alter their decisions regarding food item choice, developing a preference for the food item colour that offers the greater pay-off. As these pay-offs only

differed in the context of caching and not consumption, subjects seemed to be developing a colour choice preference based on overall pay-off benefits. Over the course of the experimental condition, where caches were removed, the overall choice for the non-removed food items became stronger. Although subjects altered their food colour type choice, we observed no difference in the spatial arrangement of caches for the removed and non-removed food type.

Our results showed how by reducing the pay-off of a food colour type within a single context we could alter food choice behaviour in these ground squirrels. As the decision about what food colour type to choose did change over experimental presentations where caches were manipulated, we suggest that subjects were using the pay-off at cache recovery as a proxy for successive decisions with regard to colour choice. In other studies, there is still a debate as to the ability of animals to remember the content of their caches where a number of different types of food are cached (Clayton & Dickinson 1999a). We argue that the squirrels likely remember the contents of their caches and combine this with the information at recovery, that is whether a food item was there or not. The choice to avoid the removed food colour type over time might result from negative reinforcement that a specific colour offers no reward when cached. This reinforcement could arise when individuals return to an empty cache, triggering an inhibitory response through repeated negative associations (Pearce & Bouton 2001; Staddon & Cerutti 2003). This reduced pay-off when attempting to recover a removed item may cause an individual to develop some uncertainty about the overall pay-off of that food colour type (Stephens & Krebs 1986; Camerer & Weber 1992), which may then cause a shift in an individual's choice towards the food colour type that has a more certain pay-off, that is the most optimal choice (Caraco et al. 1980). The reason why we observed changes in choice in both contexts and not just caching is that subjects may assign a value to the reward and not the specific context in which the pay-off of these rewards differ (Sugrue et al. 2005). Similarly to other studies on rodents, despite the reduced item pay-off of one food type, subjects never ceased caching these unrewarded food colour types (Huang et al. 2011; Luo et al. 2014). One suggestion is that the motivational propensity to cache may be driven by an autonomous system irrespective of the costs vs. benefits of doing so (Clayton & Dickinson 1999b). Clayton & Dickinson (1999b) suggest that this compulsion to cache may be particularly prevalent when there are surplus resources or the animal is satiated, something which may be occurring in our study.

This preference for choosing the coloured food item with a positive association appeared to get stronger over the course of the manipulation condition. For exclusion abilities to be present, the shift towards picking the coloured food item type that offered the higher pay-off would have to occur after the first

manipulation presentation sessions. Therefore, rather than subjects potentially showing such advanced abilities, the behavioural changes observed maybe mediated by associative learning processes (Shettleworth 1999). Although this remains to be tested, the ability of squirrels to learn such associations may suggest they are capable of using indirect information about a reward (Nawroth et al. 2014; Nawroth & von Borell 2015), in this case whether the colour was rewarded or not, and reuse such information in successive choice presentations. This will be of biological relevance to a caching species, as a single theft event (of an item) may not characterise the future theft potential of that item (Clayton et al. 2005).

Despite squirrels developing an avoidance of the removed coloured food type over time, we observed no shift in spatial arrangement of caches for when the removed or non-removed type of food items were cached. In Merriam's kangaroo rats, theft of caches by conspecifics causes individuals to shift their cache strategy from scatter to larder hoarding (Preston & Jacobs 2001). However, unlike Cape ground squirrels, Merriam's kangaroo rats are solitary living and can aggressively defend larder stores. Due to the Cape ground squirrels' sociality, aggressive defence of a larder is unfeasible, which may explain why we see no shift in the spatial arrangement of caches. Additionally, as we targeted all caches of the removed food colour type, there was no specific pattern of cache loss, such as the complete loss of food that was placed within a certain distance of the burrow system. Therefore, there are no specific stimuli for the squirrel's to learn in relation to the success of caches placed in different spatial arrangements.

In this study, we only compared two items, one that was not removed (but experienced normal rates of cache loss) and the other with complete artificial removal. This experimental design may make the choice decisions easier as there was a clear difference between the two items in terms of pay-off. Previous studies have highlighted how in two item choice tasks, subjects can weight choices against each other, showing a preference for the item with the greatest weighting component (Yechiam & Busemeyer 2006). In our example, as this study was undertaken in the wild, we could not control for natural rates of cache loss, and therefore, the two items did not have a 1:0 pay-off ratio. However, we were able to quantify an estimate for the cache loss and show that a preference does develop overtime given this 0.44:0 pay-off ratio. Further studies in the laboratory could determine how item preference develops with a varying pay-off ratio of the two food items, to pinpoint the threshold of response (Sugrue et al. 2005).

The economics behind the decisions of what to forage on are important for animals, particularly when these decisions can have fitness implications (Stephens & Krebs 1986; Kalenscher & van Wingerden

2011). We have shown how Cape ground squirrels are sensitive to the reward pay-offs of items, shifting decisions to choose the item with a higher pay-off. These decisions appeared to form through the squirrels' ability to associate colour with a reward pay-off. As the pay-off only differed in relation to caching and not consumption, it appears these squirrels are using a general association between a colour and a delayed reward to make subsequent choices, even though this pay-off only differed within the context of caching.

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Chapter 5 (*under review in Scientific Reports*)

Use of the sun as a heading indicator when caching and recovering in a wild rodent

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Abstract

A number of diurnal species use directional information from the sun to orientate during local and global movements, possibly due to the saliency of this cue. The use of the sun in this way has been suggested to occur in either a time-dependent (relying on specific positional information) or a time-compensated manner (a compass that adjusts itself over time with the shifts in the sun's position). However, some interplay may occur between the two where a species could also use the sun in a time-limited way, whereby animals acquire certain information about the change of position, but do not show full compensational abilities. The majority of research in this area has focused on the navigational abilities of insects and birds, with a lack of data on mammals. We tested whether Cape ground squirrels (*Xerus inauris*) use the sun as an orientation marker to provide information for caching and recovery. This species is a caching, social sciurid that inhabits arid, sparsely vegetated habitats in Southern Africa, where the sun is nearly always visible during the diurnal period. Due to the lack of obvious landmarks, we predicted that they might use positional cues from the sun in the sky as a reference point when caching and recovering food items. We provide evidence that Cape ground squirrels use information from the sun's position while caching and reuse this information in a time-limited way when recovering these caches. To our knowledge, this is the first study on mammalian taxa showing what specific solar cues are used when animals orientate.

1. Introduction

Many animals use cues to orientate, whether it is following simple concentration gradients (Vickers 2000) or using celestial cues such as stars (Dacke et al. 2013). With an ecliptic daily movement across the sky, the sun is suggested to be one of the most dominant cues used by diurnal species, providing a frame of reference throughout the day (Guilford & Taylor 2014). Animals may use the sun as an orientation cue when navigating during both local (Gould et al. 2010) and/or more widespread movements (Bingman & Cheng 2005). One difficulty with using such a celestial body is that animals need to be able to demonstrate time compensation, allowing them to account for the continued shift of the sun in the sky as the earth rotates (Guilford & Taylor 2014; Gould et al. 2010). For example, homing pigeons (*Columbia liva*) have a highly developed sun compass and can account for these shifts, possibly through the perception of the arc of the sun's movement (Wiltschko et al. 2000; Wiltschko & Wiltschko 2009). Where the shifting position of the sun is not controlled for, some species may use the sun in a time-dependent manner, using fixed positional information from the sun (Wiltschko & Wiltschko 2009). However, there appears to be some interplay between both mechanisms, with some species using these cues in a time-limited manner (Guilford & Taylor 2014). This mechanism makes use of specific information that is then reused in a partially flexible way, but full time compensational abilities that account for the sun's shifting position are not present (Guilford & Taylor 2014).

For centuries, human navigators have used the sun as a compass relying on its azimuth angle, which is the angle of the sun in relation to a fixed reference, such as true north. The sun's azimuth can be used in two distinct ways, either as a compass (Perez et al. 1997), where it indicates the absolute direction with respects to the earth's surface or as a heading indicator, giving an animal a general bearing to set its movement by (Legge et al. 2014). Within familiar areas, animals may be expected to use the sun as a heading indicator instead of a compass, as solar information is often used in conjunction with habitat features (Biro et al. 2007), where the absolute direction with respect to a global position is not required. In these species, the sun may be used even with the availability of additional landmark information (Legge et al. 2014). Cue use is suggested to show a heterarchy (Sherry & Duff 1996; Waisman & Jacobs 2008), where one cue is predominantly favoured over others during different types of orientation and navigation movements. Rather than making all other cues redundant, animals may collate information, utilising a number of cues which is known as the "multiple bearings hypothesis" (Kamil & Cheng 2001). This hypothesis postulates that animals can increase the accuracy of their orientation by combining directional information from a number of

sources. In nutcrackers (*Nucifraga columbiana*), for example, it has been suggested that through use of bearings from multiple landmarks they can reduce any error they may acquire from directional information estimated solely from the sun (Kamil & Cheng 2001). Rather than making cues from the sun redundant and favouring landmark cues, diurnal species may still use celestial information due to its saliency (Gould et al. 2010).

As the sun can provide directional information, this cue can be useful for caching animals when depositing and relocating food items. There have been a number of studies to suggest that some bird species (Wiltschko & Balda 1989; Wiltschko et al. 1999) may use cues from the sun during caching events, but there are no examples of mammals explicitly using the sun in this context. Most of the caching studies have concentrated on determining whether animals use the sun through clock-shift experiments (Wiltschko & Balda 1989; Wiltschko et al. 1999), but how animals use the sun is under debate. Although it is generally accepted that the sun compass can be used in a flexible way, i.e. full time compensation (Dyer & Dickinson 1994; Wiltschko et al. 2000; Gould et al. 2010; Guilford & Taylor 2014), less is known about the degree of flexibility when the sun is used as a heading indicator, such as whether individuals can compensate for a heading angle in the reversal way. Nutcrackers (Kamil & Jones 2000) and rats (Suzuki et al. 1980, *Rattus norvegicus*) show some flexibility in finding a reward when landmark arrays are rotated whilst keeping the configuration constant. This suggests that animals may be treating landmark arrays as units of information, identifying the position of a reward within the array. Although only landmark arrays were used in these examples, the sun can potentially act as a point within a unit of an array, or it can act as a heading indicator in which to calibrate other information against (Legge et al. 2014). Furthermore, animals may show some flexibility in the use of this information if they are able to control for the movement of the sun in relation to landmark features. This can arise through simple associative learning processes, whereby individuals learn the relationship of the sun and the "visual scene", within familiar areas (Guilford & Taylor 2014).

In the Kalahari Desert, Southern Africa, where cloud cover is sporadic, the sun is a prominent feature and is continually visible throughout the diurnal period (~3730 hours of sunshine a year, global average 2334 hours, source WDC for Meteorology). In this study, we predicted that Cape ground squirrels (*Xerus inauris*), a social rodent species, use the sun as a frame of reference when navigating in the context of caching and recovering food items. We provisioned subjects with food at various points within their home range, at four time intervals throughout the day, to determine directional patterns in caching placement behaviour. When animals moved from the provisioning point to the cache point, we took GPS points of the

track they moved. From these data we were able to calculate various track properties, such as its angle in relation to the sun and the straightness. In addition, we examined recovery behaviours to determine the role the celestial system might play when subjects re-orientated back to food they had previously cached.

2. Methods

Study site and species

The study was undertaken at the Kuruman River Reserve in South Africa (26°58' S, 21°49' E), at the site of the Kalahari Meerkat Project. The reserve is located in the green Kalahari, a semi-arid region of sand dunes and flat terraces, with sparse vegetation (Clutton-brock et al. 2001). Cape ground squirrels formed colonies that were dispersed along the dry Kuruman riverbed (Samson & Manser 2015). This species is a social central place foraging rodent that lived in groups of up to 36 individuals (the largest recorded at the reserve since the study started in 2011). These groups were comprised of adult males and females (with a female bias) and a number of sub-adults, juveniles and pups of both sexes (Samson & Manser 2015). Most individuals were habituated to close human observation (less than 1m), allowing us to follow individuals whilst they foraged. Additionally, all individuals were uniquely marked using black hair dye (L'Oreal, Garnier) so that they could be individually recognised. The procedures performed in this study were approved by the University of Pretoria Animal Ethics Committee (permit number: S4532-13). All methods were carried out in accordance with the approved guidelines in this permit. In addition, Northern Cape Nature Conservation granted research permits for the study (number: ODB #1486/2013).

Data collection

Data was collected between April and July 2014 on 9 adult Cape ground squirrels across 5 social groups. Before each observation was initiated, the observer visited a social group to locate the animal. The subject was then provisioned with a single peanut in the shell and a GPS point was taken (Garmin GPS MAP62 handheld GPS device, Garmin LTD, 1996-2013, radial standard accuracy of ± 1.5 m). This provisioning point was defined as the start point of the animal's track (hereafter, start point). Subjects were provisioned with a standardized food item (2.5 cm long peanuts, in the shell) to reduce variation in behaviour caused by food of varying quality. When the animal travelled to the cache site, GPS points were taken every time an animal showed any deviation from a straight path and when the animal cached, a final GPS point was taken (the point at which the animal cached the food was defined as the end point of the tracks, hereafter, stop

point). For each observation period, subjects were provisioned with 5 nuts, following the same protocol as described above. Subjects were observed at 4 different time periods per observation day, so that any effect of time of day was controlled for. These observation periods were determined by dividing the time between sun rise and sunset by 5, giving 4 time points with mean ± SD start times of; 8:46:46 (h:m:s) ± 5.52 minutes, 10:59:13 ± 1.46 minutes, 13:11:40 ± 4.06 minutes, 15:24:07 ± 8.41 minutes. As the sunrise and sunset times constantly change, these periods were calculated for each day, enabling us to conduct observations at the same relative time each day. As the subjects got up after sunrise and went below for the evening before sunset, these periods could not be examined. For each of the 9 subjects, 3 repeats were attempted for each time period, however with some subjects this was not possible. Any missed observations were due to some subjects not being present during the period, which could be due to the subject being below ground (for the 1st observation period) or the subject could not be found.

Calculation of track angles

Initially for each of the 5 groups, a hypothetical caching area boundary was determined using the GPS point of the cache placed furthest away from the centre of the home burrow as the radius length for the circle. The angle of the sun (hereafter the azimuthal angle) in relation to the centre of the burrow was extrapolated to this boundary line and the coordinates calculated. The azimuthal angle was calculated using data obtained from SunEarthTools (www.sunearthtools.com, see supplementary Fig. S1 for an example). The position of the sun was calculated for the exact date and time of the tracks using coordinates of the centre of the home range associated with each subject to obtain these measurements. The track angles were then calculated by extracting the angular difference (in radians) between the cache track and the azimuthal angle of the sun (see supplementary Fig. S2).

Statistical analysis

All statistical analyses were performed in R; release GUI 2.1 (R Core Team 2015). Linear mixed effects models (hereafter, LMM,, Bates et al. 2014) were performed using the "lme4" package in R for all models as this allowed us to include random effects. To control for variation in these parameters, we included subjects nested within group as random factors. To determine the significance of fixed effects, we used likelihood ratio tests (hereafter, LRT, Crawley 2007) to compare LMMs with and without these effects. For comparisons of distributions, we used Kolmogorov-Smirnov tests (hereafter, KS-test).

Distribution of track angles in relation to the sun

The raw data for angular differences from the sun were transformed, so that all values were in relation to 0 radians (analogous to the angle of the sun). In doing so, the data were bounded between -1/2π radians and 1/2π radians, with the minus values corresponding to tracks that moved to the left of the sun's azimuth. As the data were analysed in this way, circular statistics (Batschelet 1981) were avoided, and we did not need to control for issues arising from data being on a true angular scale. In addition, as we recorded more than one track per subject, post-hoc mixed modelling allowed us to control for repeated measures, deal with the unbalanced design and control for subject and group variation. A dip test ("diptest" package, Maechler & Ringach 2013) was performed on the distribution of raw data to determine the number of modes, which suggested the distribution of angles showed non-unimodality. We then ran a finite mixture model using an expected maximisation (EM) algorithm to determine parameter estimates for the components of the multimodal distribution observed ("mixtools" package, Benaglia et al. 2009). To extract the standard error (SE) for each parameter estimate, we bootstrapped the mixed model (Peel & MacLahlan 2000, B = 2000). This provided us with SE estimates for the lambda (proportion of overlap of the two distributions), mean and standard deviation for each.

Patterns of the component distributions

The component distributions extracted after running a finite mixture model were compared using KS-tests and LMM's. To compare distributions, we examined the differences by inverting the values of the distribution where tracks were made to the left of the sun (at negative radian angles), which put both on the same scale. We then ran a KS-test on the data to determine if there were overall differences in these two component distributions and then ran an LMM to determine whether there were differences in the size of track angles between the two. Finally, we ran LMMs to identify if the angle values for each distribution were significantly different from zero (i.e. the angle of the sun).

Examining across observation periods

To determine whether the track angles changed with the shifting angle of the sun, we ran an LMM, with the absolute angle of the sun as a fixed effect. As a response, we used the track angle in relation to the angle of the sun at a given time point. If subjects were using the sun as a heading indicator similarly across observational time periods, then the azimuthal angle difference between the sun and track should remain constant, as the sun moved along its arc of trajectory.

Track straightness

We used the "move" package (Kranstauber et al. 2013) in R to determine the track length made by an animal when moving from the start to the stop points. The Euclidean distance between the start and stop points was then calculated, which gave us the shortest distance between the two points. We then calculated the 'straightness index' (Batschelet 1981), which is the Euclidean path length divided by the observed path length, where a value of 1 would suggest a track was straight and 0 where a track was highly tortuous.

Recovery success and time

In addition to using the sun as a heading indicator when caching, we investigated if caches were recovered using cues from the sun. We examined the fates of caches (n = 47) by setting up remote cameras (5210A series, LTL-Acorn Outdoors) near the cache site for 5 days and recorded 15-second videos whenever the infrared component was triggered. This allowed us to calculate the time lag between caching and fate, for both stolen caches and those recovered by the cacher. For recovered caches (n = 20), we calculated the azimuthal angles of the sun in the sky when the caches were made and when they were recovered. As the time and location of the recovered cache was known, we were able to calculate the accurate local azimuthal angles of the sun for the recovery event using the method described previously for the azimuthal angles at caching. Due to the fact that this is a social species, there is a high risk of caches being stolen (87.5% of caches that were stolen were done so within 24 hours (n = 24) and 57.4%, of caches were stolen in total (n = 27)) and therefore subjects may recover within 24 hours to reduce the likelihood of cache theft. As a number of caches were recovered within 24 hours (n = 12, 60%, overall caches had a mean recovery time of 16.03 ± 5.84 hours, mean ± sd), we hypothesised that subjects may show some flexibility in their use of the sun, but not show full time compensation.

As the sun's orbit along the arc of trajectory is symmetrical about the North-South plane (the sun's zenith), the azimuthal angles of the sun therefore also show symmetry (Fig. 1b). We compared the azimuthal angle of the sun in relation to the centre of the groups burrow at recovery to both the azimuthal angle at 24 hours after the cache and the opposite azimuthal angle to this 24-hour point (Fig. 1b). Any caches that were recovered closer to this opposing rather than the 24-hour position were categorised as being recovered at the pre-24 hour point, hereafter PRE24hr. Any caches that were recovered closer to the 24-hour point were categorised as being recovered at the 24-hour point, hereafter A24hr. Using this data, we were able to examine the relationship between the recovery and cache azimuthal angles using LMMs, with the recovery

angle as the response and cache angle as a fixed effect. The differences between angles at caching and recovering were extracted to determine how accurate subjects were at recovering caches at the PRE24hr and the A24hr categories at varying elevation angles of the sun. Furthermore, we examined this difference to determine what the effect of the sun's elevation at the point of caching had on recovery accuracy.

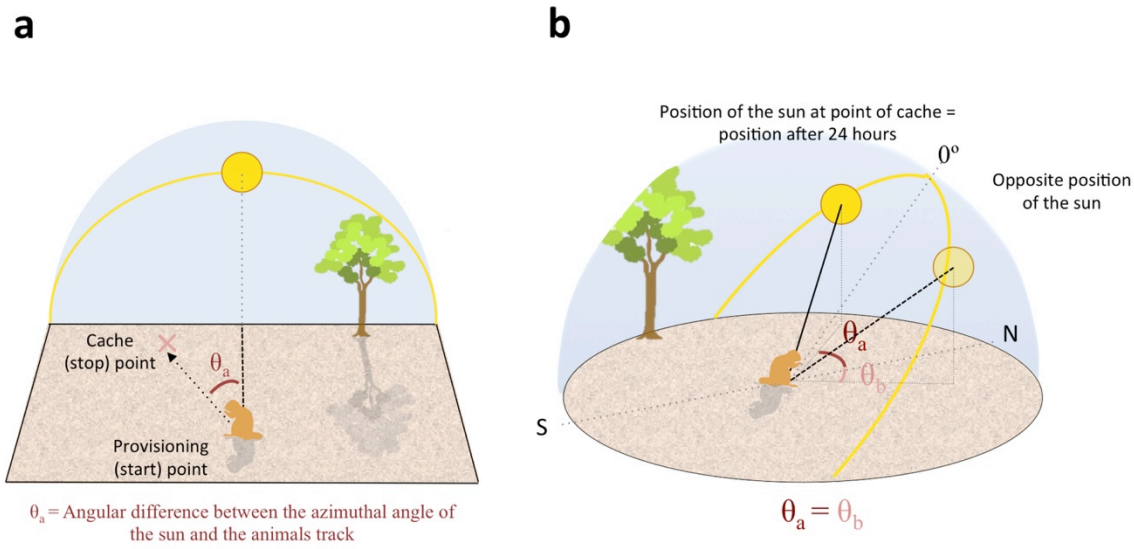

Figure 1: A diagrammatic representation of how the track angles were calculated (see also supplementary Fig. S2, **a**). An illustration of the path of the sun through the sky and how the azimuthal (and elevation) angles are the same when you consider opposite positions of the sun on its arc, **b**. Any caches recovered close to the 24-hour point (θ_a) were defined as being recovered within the A24hr category. For caches that were recovered closer to this opposite azimuthal angle of the sun (θ_b), they were defined as being recovered within the PRE24hr category.

Foraging areas

The areas of the start points were calculated for each subject by identifying the minimum convex hull of these points ("alpahull" package, Pateiro-López & Rodrıguez-Casal 2009). The areas of the hulls were determined by setting the alpha value of the hull at the minimum value where all boundary points were covered. The area was then extracted using an inbuilt package function. A hypothetical foraging area was determined by calculating the maximum distance at which start points were recorded from the burrow for

each subjects and using this as the radius to calculate the area (mean ± SD, 34.4 ± 29.7 m). If subjects homogenously distributed themselves throughout their home range, the area of the hulls should not differ from that of the hypothetical area.

3. Results

Track angle patterns

The angles of the tracks in relation to the sun were plotted and the distribution of angles showed bimodality (Hartigans' dip test; D = 0.03, *P* = 0.042, Fig. 2a). As no difference was found in the distribution of track angles depending on whether subjects moved towards or away from the sun (KS test; D = 0.10, *P* = 0.760), we pooled data to model absolute track angles. This lack of difference between the two previously described distributions further justified why these results could be analysed without the need for circular statistics. We found that the component distributions extracted from a finite mixture model (Fig. 2a) were significantly different (KS-test, D = 0.21, *P* = 0.001), with the track azimuthal angles of the distribution to the left of the sun being larger than the azimuthal angles to the right (LRT, v_1^2 = 10.48, *P* = 0.001, Fig. 2b). In addition, the means of both distributions significantly differed from zero (Fig. 2b, left distribution (i.), (mean ± sd) -1.01 ± 0.05, LMM, t_{126} = 19.45, *P* < 0.001, right distribution (ii.), 0.59 ± 0.06, LMM, t_{223} = 19.75, *P* < 0.001) suggesting that subjects tended to move at angles to the sun, rather than directly towards/away from it. Although neither distribution significantly differed from a probabilistic normal distribution ((i.), KS test; D = 0.52, *P* = 0.977, (ii.), KS test; D = 0.72, *P* = 0.558), both were platykurtic displaying negative kurtosis values ((i.) = -1.25, (ii.) = -0.97). Examining these track azimuthal angles from the sun across observational periods, we observed that the angles changed in relation to the shifting positions of the sun in the sky (LRT, v_1^2 = 97.80, *P* = < 0.001). In addition to this, relative azimuthal angular differences from the sun and tracks did not differ across observational periods suggesting subjects were moving at consistently similar offset angles throughout the day (LRT, v_1^2 = -0.47, *P* = 0.239).

How straight are tracks?

The angles of the tracks are only relevant if the subjects move in a near linear manner, i.e. move in a straight line from the start point to the stop point. The straightness index for the tracks was (mean ± sd) 0.89 ± 0.15 (see supplementary Fig. S3 online), and the distribution of index values was heavily left skewed towards 1 (skewness value = -1.54).

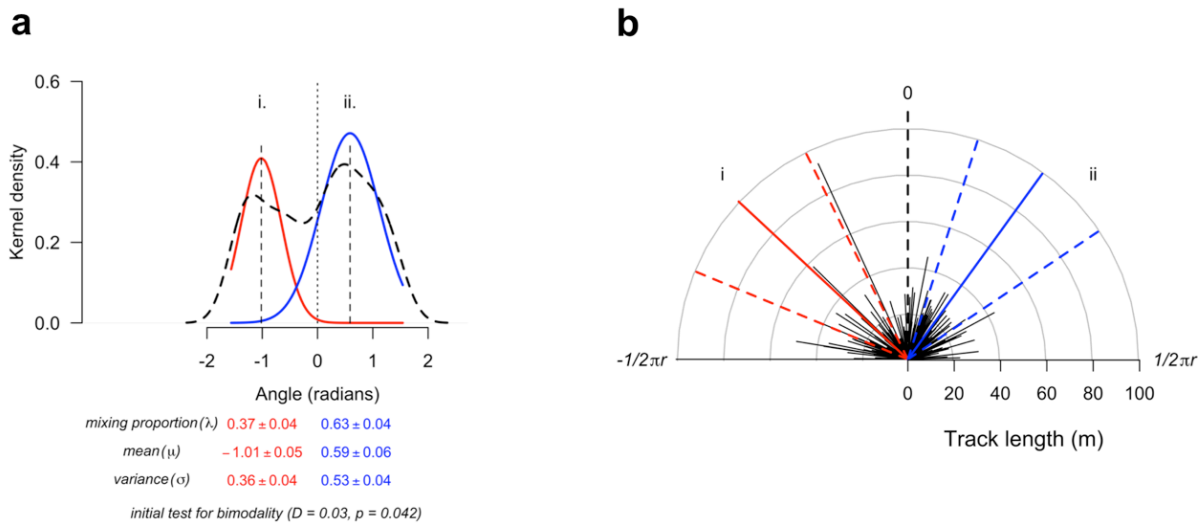

Figure 2: The observed bimodal distribution of track angles from the sun (dashed line, N = 265) and two distributions extracted using a finite mixture model (two-component distributions were identified, red (i.) and blue (ii.), **a**). An angle of 0 radians would mean the subject moved directly towards or away from the sun. The values beneath the plot represent bootstrap estimates of the standard error for each summary statistic. Visualisation of how the track angles (mean ± sd, solid and dashed coloured lines respectively) of the two mixture distributions differed from the angle of the sun (represented as 0, **b**). Straightened observed track angles and lengths are shown in black.

Caching and recovery times

The survival times of caches were negatively related to the number of individuals in a group, with more individuals leading to a reduction in the time until a cache was stolen (LRT, v_1^2 = 6.86, P = 0.009). The recovery time for caches was 16.03 ± 5.84 (mean ± sd) hours, suggesting subjects were not solely relying on the position of the sun 24 hours later to recover. Caches were equally as likely to be recovered in the PRE24hr and A24hr categories (proportion tested = number of caches recovered in the PRE24hr category: total number of caches recovered, proportion test: X^2 = 0.45, P = 0.500). The decision about when to recover a cache may be influenced by a subject's resident group size, where the number of individuals present was higher for when caches were recovered during the PRE24hr as supposed to the A24hr category (LRT, v_1^2 = 5.81, P = 0.016, Fig. 3a). When subjects recovered within this PRE24hr category, they did so when the sun was at the same azimuthal angle in the sky as the position during caching, but at the opposite point on its arc of trajectory (Fig. 1b). Where caches were recovered in the A24hr category, they were more likely to be recovered near the 24-hour point. The relationship between these caching and relative recovery azimuthal

angles of the sun was strongly significant (LRT, v_1^2 = 12.64, P < 0.001, Fig. 3b), suggesting subjects were recovering at the same relative elevation angle as during caching. The error, in terms of the differences in angle at caching and recovery were significantly smaller for lower elevation angles of the sun (LRT, v_1^2 = 4.48, P = 0.034, Fig. 3c), but we found no difference in error depending on whether caches were recovered in these PRE24hr or A24hr categories (LRT, v_1^2 = 0.01, P = 0.947).

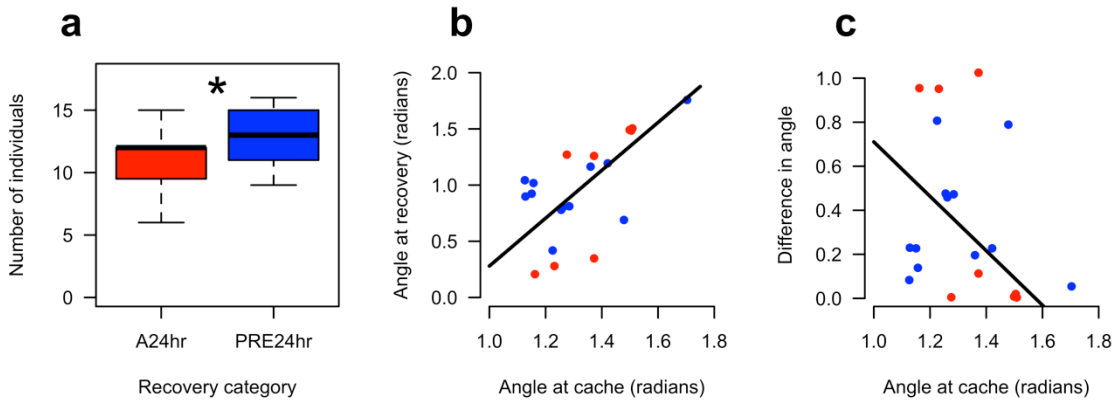

Figure 3: The influence of the number of individuals present in a group on the recovery times of caches, **a**. The relationship between the relative angle of the sun in the sky at caching and recovery, **b**. How the difference between the sun's azimuthal angle at caching and recovery was affected by the elevation angle of the sun at caching, **c**. Red points represent caches recovered within the A24hr and blue points the PRE24hr category.

Size of foraging areas

The total null foraging area was significantly larger than the start point area, suggesting subjects were not homogenously found throughout a home range (LRT, v_1^2 = 27.74, P < 0.005, mean % of total area covered by start points = 12.25 ± 7.18 %, mean ± sd). This indicates that subjects foraged within a preferred area around the central burrow and showed a clustered distribution within the overall null area.

4. Discussion

Although it is widely known that some animals rely on the sun for navigation, how they do this is still very contentious (Guilford & Taylor 2014). Here we demonstrated that Cape ground squirrels might use the sun as a heading indicator, moving in near-linear lines, at consistent offset azimuthal angles from the sun. We suggest these behaviours allow individuals to gather information about the location of where they cached an item and reuse this information in recovering the food. As individuals have the ability to recover food within 24 hours, we propose that individuals show some flexibility in their reuse of the sun's information. However, as this does not show a level of flexibility required for full time compensation, the ability to fully control for the shifting position of the sun throughout the diurnal period, we propose these ground squirrels are reusing heading information from the sun in a time-limited way.

When Cape ground squirrels moved from start to stop points, when caching food items, they appeared to move at azimuthal angles that were offset from the position of the sun, irrespective of whether they moved towards or away from the sun. We suggest that rather than making tracks with random angles in relation to the sun, subjects moved at consistent angles every time they placed a cache. Combined with the result that tracks were straight, individuals may be using simple rules, moving in near-linear directions at similar offset azimuthal angles from the sun to deposit a food item. These behaviours suggest that the sun was potentially being used as a heading indicator rather than a compass (Guilford & Taylor 2014), where individuals utilise the azimuthal angle of the sun, possibly in relation to other habitat features. The consistency of the track angles from the sun may allow for individuals to more easily obtain information about the track, rather than moving at random angles that would need to be memorised each time a cache was made. The reason for why these angles are offset from the absolute position of the sun may be due to solar glare, which could impact on an individual's ability to monitor their environment (Carr & Lima 2014). In our example, monitoring the environment can refer to the ability to detect predators (Fernández-Juricic & Tran 2007; Carr & Lima 2014) or gathering spatial information (Wolbers & Hegarty 2010) about where a cache is being located.

As Cape ground squirrels are central place foragers with observed preferred foraging patches we assumed that individuals would be familiar with landmark arrays around their home burrow. In homing pigeons, it was suggested that the mechanisms of foraging in unfamiliar areas are different from familiar areas (Holland 2003), where individuals may develop a "familiar area map" (Baker 1982). With these features, animals are predicted to develop a map based on memory of familiar landmarks. In addition, within

such familiar areas, individuals may be able to learn how the path of the sun in the sky relates to landscape features, via associative learning processes (Guilford & Taylor 2014). We argue that in our study, individuals were using celestial information and memory of their foraging patch to locate the start point of a previous cache track. The endogenous circadian clock (Edery 2000) may allow for individuals to move to this start point at the appropriate time (Bienach et al. 1991; Petruso et al. 2007; Guilford & Taylor 2014), where they then reuse heading information from the sun to move to the cache site.

Due to the sociality of this species, cache food stores are prone to high levels of theft (Vander Wall 1990), and we found a large number of caches were stolen within 24 hours. This may lead to selection for mechanisms that allow ground squirrels to recover food within 24 hours. Theft of caches in social living animals has been linked to the number of individuals in a group, where random foraging movements of conspecifics may lead to competitors uncovering caches more rapidly (Stone & Baker 1989). In our study species, individuals have been shown to exhibit sensitivity to audience numbers by reducing the amount they cache, consuming the food item instead (JS unpublished data). In the current study, this fluctuation in competitor number explains why some caches were recovered before the 24-hour lag period. The ability to recover flexibly between the two time periods in response to an increase in competitor number could be driven by hormonal changes in the cacher. For example, cortisol has been shown to increase with group size (Pride 2005) and has also been implemented in causing changes in caching behaviour (Saldanha et al. 2000).

The ability of animals to show full time-compensation in their use of the sun is thought to be mainly restricted to specialist navigators/orientators (Dyer & Dickinson 1994; Guilford & Taylor 2014), and therefore assumed not to occur within these squirrels. Rather, individuals may be reusing certain information from the sun in a 'semi-flexible' way, i.e. they are showing time dependency (Wiltschko & Wiltschko 2009) by recovering food around the 24-hour point, but additionally recovering food at a point pre-24 hours. When food was recovered within 24 hours, individuals were recovering when the sun was at the same elevation angle in the sky as the cache point, but on the opposite position of the sun's arc. Individuals may be able to recover food at this point by compensating for the reversal of the sun's position, potentially within a landmark array. Studies have shown how some species can account for a reversal in landmark arrays, by treating landmarks as units rather than individual elements (Suzuki et al. 1980; Kamil & Jones 2000). However, how the subjects used this alternate position of the sun remains to be tested, as the animal's endogenous circadian clock may only allow them to recover at 24 hours, i.e. in a strictly time dependent way. One suggestion is that the squirrels have a limited "solar ephemeris function", which allows the subjects to

control for the changing position of the sun throughout the day, where in this example, only the relative azimuthal angles of the sun are used (Petruso et al. 2007). The use of the sun in this way could suggest individuals show an adaptively specialised learning mechanism that is problem-specific (Gazzaniga 2000; Towne 2008), where only fixed points on the solar ephemeris can be utilised.

Although we argue that Cape ground squirrels use the sun as a heading indicator whilst caching and recovering, a number of studies have suggested this cue has to be used in combination with other information, such as landmarks (Kamil & Cheng 2001; Gould et al. 2010). This study was undertaken in the squirrel's natural habitat and therefore, manipulating landmarks was unfeasible. Additional experiments examining the interplay between landmark and celestial use would help us determine how individuals use these cues in combination to deposit and relocate caches. Subjects appeared to be able to recover food items even with angular error in the position of the sun at recovery compared to the position at caching, suggesting additional cues may be used, such as landmarks. The "multiple bearing" hypothesis (Kamil & Jones 2000) states that rather than an animal using a single cue and making others redundant, individuals can use a multitude of cues to increase spatial accuracy. In this study, error could result from the inability to accurately determine the angle of the sun at various time points in the day. For example, we saw that the difference between caching and recovery angles was greater when the sun was at greater elevation angles in the sky. This is in line with a study on homing pigeons, where orientational precision decreased as the elevation angle of the sun increased towards the zenith (Wiltschko et al. 2000).

Although discussed within the context of caching behaviour only, the evolution of such an orientation system could also be linked to general foraging behaviour. In the Kalahari, food is dispersed and sparse, but occasionally bonanza resources are located and these are often clumped. For example, bulbs of the bushveld vlei lily (*Nerine laticoma*) and the fruiting body of the tsamma melon (*Citrullus lanatus*) are sporadically uncovered or sprout within the foraging range of a group. Therefore, it may be beneficial for an individual to memorise the location of such a patch, which can then be visited on successive foraging forays (Held et al. 2005). The mechanism by which the location of these patches could be acquired would be similar to what is described for caching behaviour, whereby individuals utilise cues from the sun and possible landmarks that would enable individuals to re-orientate back to that patch.

To our knowledge this is the first study on wild mammals to describe such strategic use of the sun in this way. In general, our study sheds light on the interplay between time-compensated and time-dependent

use of the sun as a heading indicator. We suggest that this flexibility may have evolved due to the high risk of caches being stolen, and that this study species has developed a problem specific strategy to reduce this theft. The time-limited use of the sun identified in these squirrels may encourage other studies on species that display time-dependency to examine to what degree this behaviour is flexible, and how it is manifested in subsequent behaviour.

5. Acknowledgements

We thank Tim Clutton-Brock, David Gaynor and the Kalahari Research Trust for support and access to work on the Kuruman River Reserve and Northern Cape Nature Conservation for the research permits (number: ODB #1486/2013). We also thank the volunteers on the squirrel project for their help collecting the ad libitum data on the squirrels and Nicola Harrison, Patricia Lopes and Alex Thornton for their constructive comments on earlier drafts of the manuscript. The maintenance of the study population and collection of basic data was financed by the Universities of Cambridge and Zurich. JS and MBM were both financed by the University of Zurich. All procedures performed in this study were carried out in accordance with the ethical standards of the University of Pretoria Animal Ethics Committee (S4532-13).

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7. Supplementary material

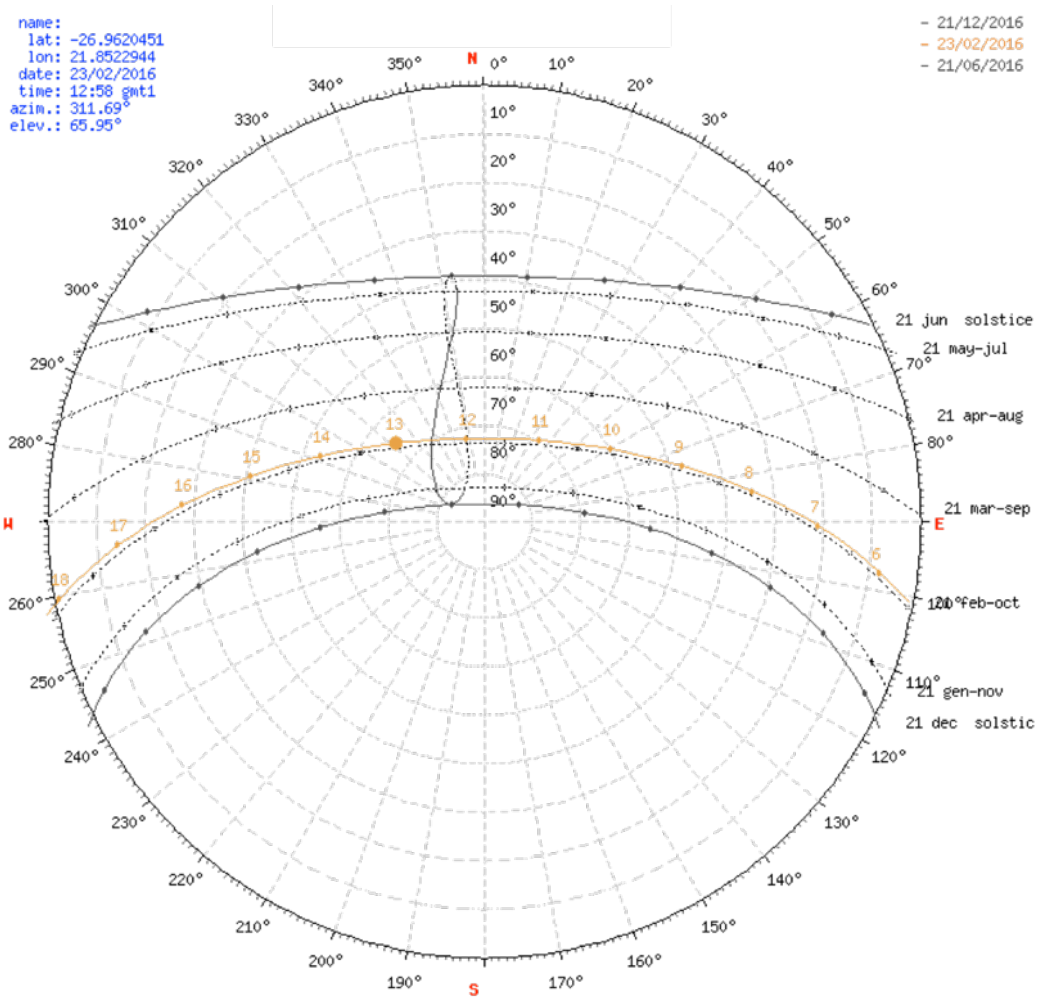

Figure S1: An example of the diagrams extracted from the SunEarthTools repository. For each group, we used the coordinates of the centre of the sleeping burrow to obtain the local path of the sun in the sky. In addition, we used the precise time and date of the track to obtain an accurate measurement of the angle of the sun at this time.

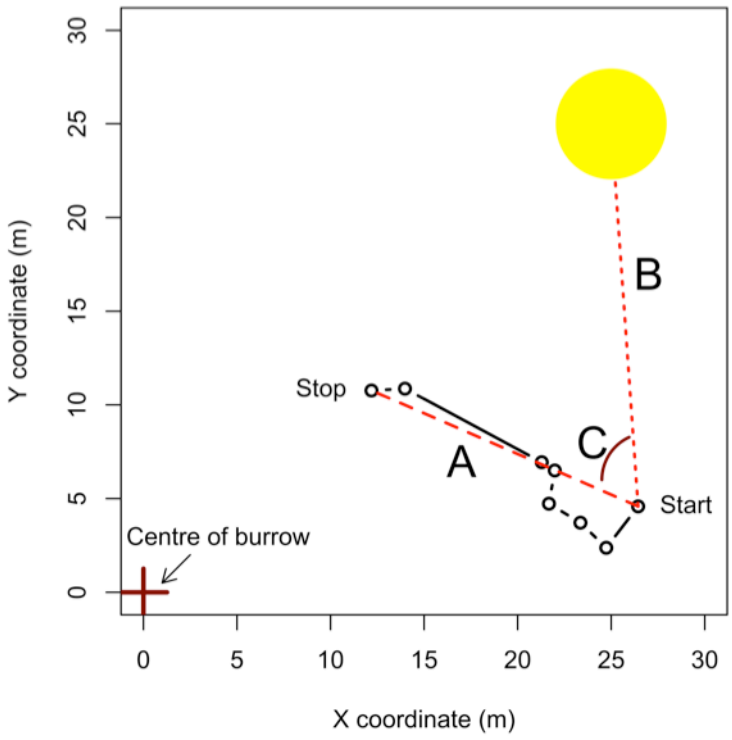

Figure S2: How the azimuthal angle between the sun and track was calculated. The local sun diagrams from Fig. S1 were overlaid on the groups home range and then both the angle of the sun and the points of the track were calculated in relation to the centre of the home range (0,0). As tracks were significantly straight in form, we were justified in using the Euclidean distance between the start and stop points of the tracks to allow for the calculation of the azimuthal angle.

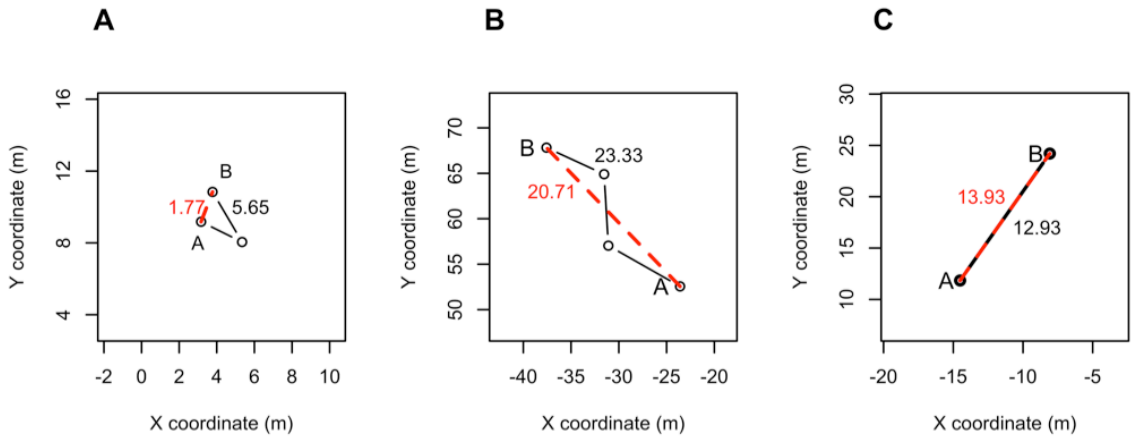

Figure S3: Examples of tracks of varying lengths (lengths, in metres, donated by the numbers) and straightness; highly torturous (a), average tortuosity (b), straight (c). The tortuosity was calculated using the "straightness index"[1], which is the Euclidean distance (red) divided by the observed distance of the tracks (black).

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Conclusions and outlook

1. General discussion

In this thesis I investigated the decision-making and cache protection strategies in the social living rodent, the Cape ground squirrel (*Xerus inauris*), through observations and experiments conducted in the wild. Natural caching appeared to be highly seasonal in this species with peaks occurring just after the onset of the heaviest periods of rainfall. Although no sex differences were found in natural caching behaviours, there were clear age effects on the intensity of caching. Due to the dispersion of caches around a central sleeping burrow, this species is defined as a scatter-hoarder (Vander Wall 2003). As this type of cache strategy reduces the ability of an individual to aggressively defend food stores due to the dispersion (Preston & Jacobs 2001), it is assumed individuals will engage in a number of different alternate tactics to ensure cache survivability. Caching is only an adaptive behaviour when the benefits in terms of recovering a food item out weigh the costs in terms of energy expended in caching and also loss to competitors (Andersson & Krebs 1978; Stapanian & Smith 1978). The direct influence of competitors appeared to play a key role in shaping ground squirrel behaviour. Firstly, I showed that competitor number caused individuals to reduce the investment they made in caching food, preferring to consume food instead. Secondly, the behaviour of conspecifics that were nearby a cache event were analysed which highlighted how cachers are sensitive to the attentive state and not just the presence of these individuals. Besides social effects on caching behaviour, I looked at the profitability of the food that individuals cached to determine if individuals were flexible in their decisions about what to cache. Individuals appeared to alter their caching behaviour in response to differential item payoff, investing more in choosing items that had higher returns than another item. Cache protection such as being sensitive to audience attentiveness is a good strategy to reduce the risk of competitors stealing an item. However, in engaging in such behaviours, caches must also be placed in locations where the likelihood of recovery is high. In the last chapter, I show how individuals employ a number of rules in their cache placement behaviour, which may serve to increase the likelihood a cache is recovered. I highlight how cache placement is undertaken using simples rules, taking cues from the sun and potentially nearby landmarks, to aid not only in where to place caches, but also reusing this information to recover food (Wiltschko & Balda 1989; Wiltschko et al. 1999; Kamil & Cheng 2001; Gould et al. 2010). Overall, this thesis highlights a number of decision-making processes individuals must undertake when caching food to ensure maximum profitability. As this species is social, this decision-making will be highly influenced by conspecific groups members, which may had lead to the evolution of such behaviours as sensitivity to audience attentive states highlighted in this thesis. As no studies on the general cognitive capabilities of this species have been conducted, I argue the decision-making processes described throughout this thesis are the result of

multifaceted learning mechanisms and not driven by cognitive mechanisms. These behaviours, although examined in the context of caching in this thesis may be used in more general foraging tactics to alleviate competition from or to reduce agonistic interactions with conspecifics.

2. Cache patterns and when to cache

The first two themes examined in my thesis were what were the patterns of caching and how the social environment affected caching decisions (figure 1). The first theme considered when caching occurred in terms of environmental, ontogenetic and demographic influences and the second theme focused on when individuals cached in relation to the behaviour and presence of conspecifics. The motivation to cache is driven by a number of factors in a range of species, for example European lynx (*Lynx lnyx*) store carcasses in trees to protect kills from competitors (Cerveny & Okarma 2002) and grey squirrels (*Sciurus carolinensis*) store acorns as a supplement during harsher periods (Hadj-Chikh et al. 1996). In **chapter 1**, I described the spatio-temporal patterns of caching by the Cape ground squirrel, using data from a long-term project. Caching intensity increased just after the heaviest bouts of rain, which suggests that caching in these squirrels is linked to resource availability (Lucas 1994). I also quantified the spatial patterns of caching in this species, showing that caches were dispersed throughout the groups' home range. This scatter-hoarding strategy is predicted, as defence of single store will be unfeasible against a superior competitor (Suselbeek et al. 2014). Unlike in other rodent studies, a switch between larder and scatter-hoarding is not observed in these ground squirrels, possibly due to the inability of individuals to aggressively defend cache sites (Preston & Jacobs 2001; White & Geluso 2012). In their study on magpies (*Pica pica*), Clarkson et al. (1986) highlight the trade off between dispersing caches to reduce conspecific cache theft and hyper-dispersing caches to the point caching becomes unviable. Using model equations from Stapanian & Smith (1978), I described how cache placement in relation to the central burrow system occurred optimally where the benefits in terms of the increased recovery of food outweighed the costs in terms of caching food (**chapter 2**). Such optimal spatial placement of caches highlights a way in which ground squirrels may try to maximise the payoffs from their caches and thus fitness through economic decision making processes.

When to cache is an important consideration for a social species as due to the constant presence of competitors the cost of caching may be high due to an increased risk of cache loss (Vander Wall 1990). Animals can respond to the presence of conspecifics by engaging in certain behaviours to minimise cache

loss (Dally et al. 2006). In my thesis I have shown a number of ways in which animals make flexible decision on when to cache based on the number of competitors and their attentive state. The number of conspecifics present in a group affected the decision about when to cache (**chapter 2**). Although such behaviours have not been described in other rodent species, the preference to consume rather than cache food in response to increased social pressure has previously been shown in nuthatches (*Sitta europaea*). Instead of suggesting individuals are capable of complex numerical assessment, I argued that hormonal changes linked to a fluctuation in competitor number (Pride 2005) were causing the variation in the decision to cache or consume a food item (Saldanha et al. 2000). In mountain chickadees (*Parus gambeli*), corticosterone was shown to cause individuals to recover more efficiently and visit more caches sites. Due to there being no effect of dominance, distance from the burrow or density of caches on cache survival rates, individuals may not experience the necessary selective forces to cause changes in these behaviours (see examples; Hampton & Sherry 1994). Unlike in **chapter 2**, where delayed cache loss was studied, the results from **chapter 3** were linked to the risk of immediate cache loss, when conspecifics were nearby to cache events. The risk of immediate cache loss appeared to be linked to the attentive state of nearby conspecifics. In contrasts to other studies on rodents (Preston & Jacobs 2001; Steele et al. 2008; Hopewell & Leaver 2008) these ground squirrels were displaying sensitivity to specific conspecific behaviours and not merely their presence/absence. Such response to the knowledge of audience members during caching events has only previously been described in a small number of bird species such as ravens (*Corvus corax,* Bugnyar & Heinrich 2005) and mountain chickadees (*Poecile gambeli*, Pravosudov 2008). Unlike delayed cache loss, individuals who experience immediate competition over a cache may learn over the outcome of repeated interactions how their behaviour and dominance may affect the result of these competitions. Some studies on response to attentive states of others have suggested that these species may show advanced cognitive capabilities, understanding what a competitor may know about an event (Thom & Clayton 2013; Dally et al. 2004; Bugnyar & Heinrich 2005; Dally et al. 2005). I argue against this cognitive underpinning in the Cape ground squirrels and suggest their response to attentiveness develops over repeated interactions with conspecifics leads to associatively learnt aversions. These interactions may occur during both caching and general foraging where competitors try to compete with an individual for a food item. From these two studies the decision making of when to cache appears to be highly flexible, with individuals altering their behaviour based on aspects of the social environment.

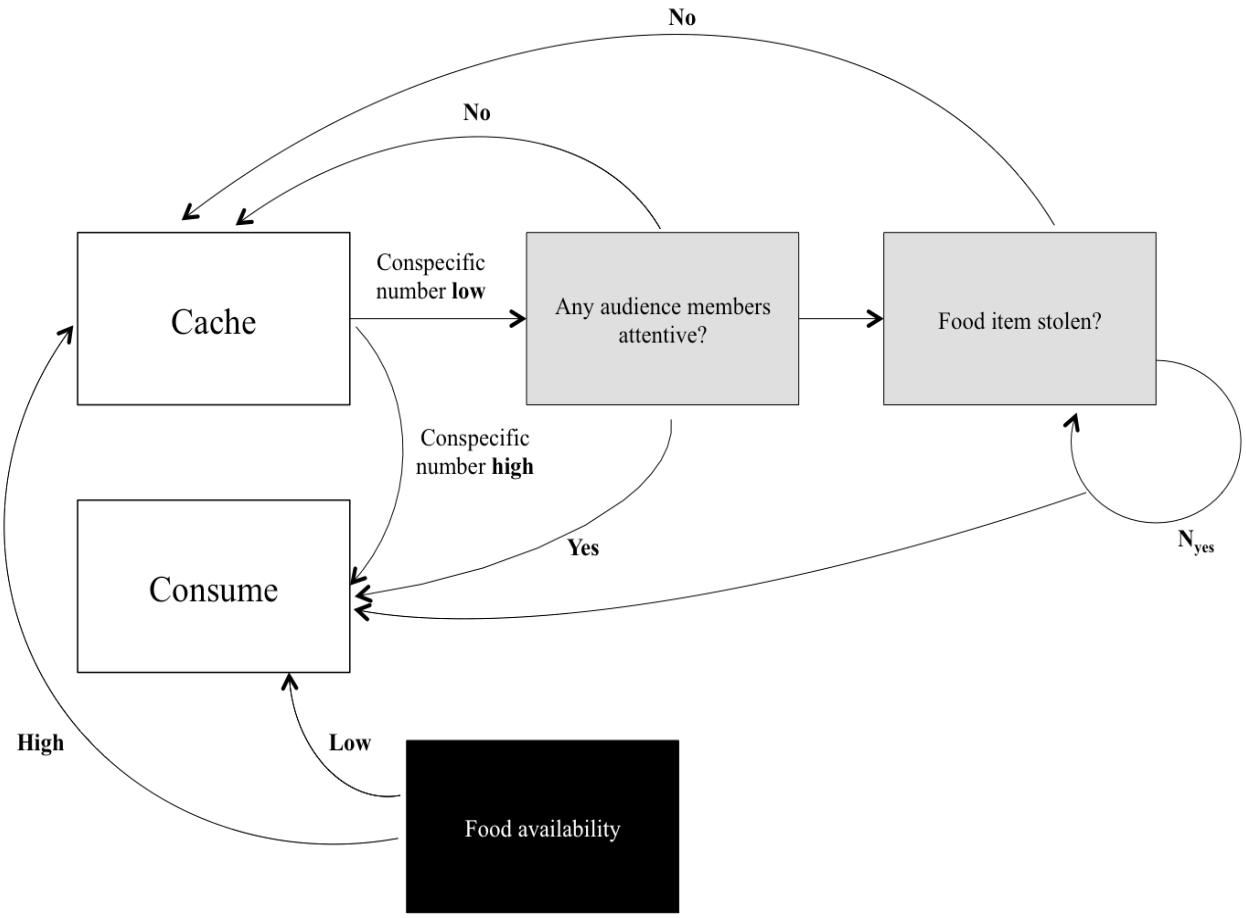

Figure 1: A basic representation of the cache decision-making processes for Cape ground squirrels. The factors affecting decisions are split in to two categories: 1. Social influences (filled grey) and 2. Environmental influences (filled black). When a food item is stolen, the decision of whether to consume an item will be influenced by repeated reinforcement of the reduced survival of an item.

3. What to cache

Animals may make a number of different decisions when caching a food item and through repeated cache loss, individuals may become sensitive to what they are caching (Busher 1996). For example, items that quickly degrade or are frequently stolen (Clayton et al. 2005) are not profitable to cache and individuals may therefore favour alternate items where available, which offer greater rewards. In **chapter 4**, I tested whether individuals would alter their caching investment in two food items, one of which had a larger pay off than the other. Response of individuals to show immediate preference for a higher payoff choice may suggest a species has "exclusion performance" ability (Schloegl et al. 2009; Schloegl 2011; Nawroth et al. 2014). An underlying assumption of this behaviour is that is should occur spontaneously, as learning payoffs over time

may suggest learning processes are involved. Subjects in my study showed a preference for overall choice of items that had a higher payoff, rather than reducing investment in caching items with the lower return. I argue that a complex decision making paradigm is occurring with individuals learning over time what food offers the best returns when cached and then altering their choice behaviour in subsequent trials. This choice about what to choose appeared to develop over time, which suggests that the decision-making processes underpinning this choice are shaped through repeated choices, with learning processes being involved (figure 1). Such response to varying the cache payoffs of a single item within a multi-item choice framework has only been previously studied in Western scrub jays (*Aphelocoma californica*, de Kort et al. 2007). Studies on rodents have been confined to determining the effect of complete cache pilferage, where all items are experimentally removed (Huang et al. 2011; Luo et al. 2014). These studies have highlighted how rodents are sensitive to this level of cache loss and similar to my study appear to learn the reduction in cache payoff over time. In human behavioural economics, this type of choice behaviour is known as "prospect theory", whereby individuals weigh the probabilistic risk of an activity against another (Kahneman & Tversky 1979). In our example, a variant of this behaviour may occur, whereby individuals are weighting the risk of one item being stolen (and thus not recoverable) over the other, where the non-removed food items provide better overall pay-offs. How these choices develop could be a result of an interplay between hormonal and behavioural mechanisms impacting on value based decision-making as had been suggested by Sugrue et al. (2005) (figure 2).

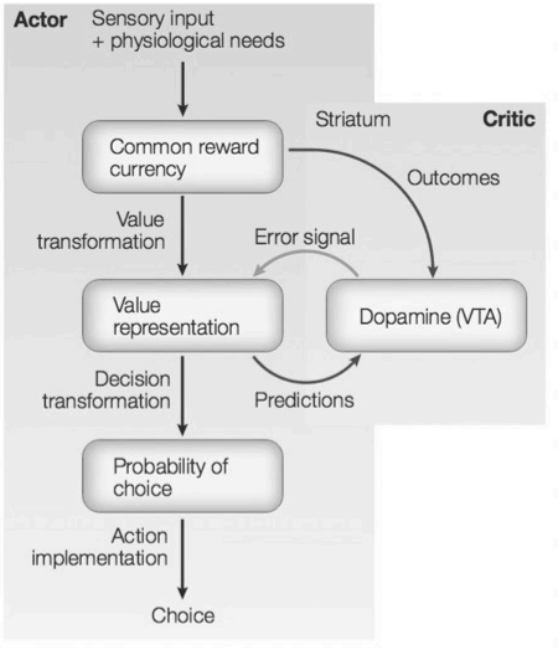

Figure 2: Conceptual framework ("actor-critic" architecture) for simple value-based decisions (*reproduced from* Sugrue et al. 2005)

4. Where to cache

When a food item is deposited in a cache, animals must memorise the location of the cache in relation to the surrounding habitat (Gould et al. 2010). In scatter-hoarders where food is dispersed (Vander Wall 1990), individuals must remember the location of a number of food items (for example the pinyon jay *Gymnorhinus cyanocephalus*, Bednekoff & Russell 1995). Animals will therefore often use external cues which act as reference points allowing for an individual to recall the location(s) of a cache(s) within a given home range (Kamil & Cheng 2001; Gould et al. 2010). Due to its saliency at the study site I examined whether animals acquire and use information from the sun when caching (**chapter 5).** Here I provided the first example of how a mammal can use cues from the sun during caching and recovery behaviours, where existing studies have been confined to scrub jays (Wiltschko & Balda 1989; Wiltschko et al. 1999). In their review of the use of the sun as a navigational tool, Guilford & Taylor (2014) argue for an intermediate mechanism between full time compensation (a compass that adjusts itself over time with the shifts in the sun's position) and time-dependency (relying on specific positional information), termed time-limitation. Here I showed the first example of this intermediary mechanism highlighting the level of flexibility in ground squirrel use of the sun. Unlike specialist orientators (Dyer & Dickinson 1994; Guilford & Taylor 2014) such as homing pigeons (*Columba liva*), these ground squirrels may have a specialist form of sun-based orientation. This could have arisen through an adaptively specialised learning mechanism that is problem-specific, where only fixed points on the solar ephemeris are used (Gazzaniga 2000; Towne 2008). In previous chapters, I have shown how individuals exhibit behavioural flexibility in their responses to audience member's or food payoffs. However, with this chapter, it is clear that the use of the sun in this way does not show high levels of flexibility and therefore, I suggest that this rule following allows for individuals to recover food more efficiently. The evolution of this celestial heading system could have occurred in response to general foraging and not specifically within the context of caching behaviour. The use of the sun in this way may allow animals to memorise the locations of not only their caches, but also profitable foraging patches (Held et al. 2005) within their home range.

5. Conclusions and future research

All together this thesis has described caching patterns and explored the when, what and where decision-making processes underlying this behaviour. Cache protection strategies in rodents have received little attention, and this therefore reaffirms the importance of the studies presented in this thesis. As this species inhabits a harsh resource strapped environment and is social-living, we could expect that a number of

behaviours have evolved to reduce competition with group members. This competition may cause an "arms race", which may have led to a ratcheted-up evolution of behaviours of both cacher's and pilferers. Caching in social environment may initially seem maladaptive due to the high potential of cache theft, but as caching does occur, we can assume there is an adaptive function of this behaviour. The reason why we observe behaviours such as sensitivity to audience attentiveness and number may be as a result of selection pressure to reduce the risk of losing resources to competitors through the evolution of various cache protection strategies. As well as employing these protection strategies to limit immediate cache loss, individuals must also deposit caches in locations that reduce delayed cache loss. A trade-off is predicted to exist where individuals must disperse caches to reduce theft whilst maximising the likelihood the food will be recovered. In general, the studies in this thesis show how ground squirrels may reduce some of the costs of social living, such as increased competition for resources. Rather than displaying a pilferage tolerance strategy, it is evident from the work in this thesis that individuals try to reduce the level of pilferage suggesting caching in ground squirrels is selfish behaviour. In engaging in such protective measures, individuals maximise the payoffs from resources, something that will have fitness benefits.

Although these studies have examined decision making within the confines of caching behaviour, future work could look at foraging competitions to identify ways in which individuals alleviate competition with conspecifics. In doing so, one could track individuals throughout their life to determine how decisions change with age and therefore experience. Future research should also focus on determining the underlying mechanisms behind the cache decision making observed. Although I have argued against cognitive underpinnings, further tests such as cognitive battery testing can be employed to determine the level of behavioural complexity and flexibility this species can show.

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Courses attended

Transferable skills

Scientific writing in the Sciences and Medicine	1 ECTS
Film making for scientists	2 ECTS
Leadership competencies for PhD candidates	1 ECTS

Evolutionary Biology

Ecology & evolution journal club	1 ECTS
Advanced statistics with R - generalized and mixed effects models	1 ECTS
R4All. A recipe for success with R	1 ECTS
Conception and statistical analysis of biological experiments	3 ECTS
Topics in Evolutionary Biology	1 ECTS

Compulsory course

Other

Proximate and ultimate causes of cooperation	1 ECTS
European student conference on behaviour and cognition	1 ECTS